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The *Journal* is devoted to original research papers and notes concerning aquatic organisms or environments relevant to Canada. Review articles that are critical appraisals of broad areas of research are also welcomed. Submissions in English or French are accepted without limitations as to origin, but must not have been published or copyrighted. Details on submissions are given in guides to authors and typists at the back of each issue.

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Journal OF THE Fisheries Research Board OF Canada

Editor's Foreword

This issue of the Journal of the Fisheries Research Board of Canada is made up entirely of papers from the FRB Freshwater Institute in Winnipeg, Manitoba. The papers describe background environmental data on the "Experimental Lakes Area" of northwestern Ontario. This long-term program is designed to study effects of eutrophication (nutrient pollution) and means to control it. Because the 14 papers are so interrelated, reprints of individual articles are not available. Requests for additional copies of this issue only *should be addressed to the Librarian, Fisheries Research Board of Canada, Freshwater Institute, 501 University Crescent, Winnipeg 19, Manitoba.*

J. C. Stevenson
Ottawa 1971

Rationale, Background, and Development of Experimental Lake Studies in Northwestern Ontario[1]

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JOHNSON, W. E., AND J. R. VALLENTYNE. 1971. Rationale, background, and development of experimental lake studies in northwestern Ontario. J. Fish. Res. Bd. Canada 28: 123–128.

Reasons why experimental lake studies form a useful addition to more conventional laboratory experiments and observational field studies of eutrophication are discussed. The developmental history of the Experimental Lakes Area is given, including reasons for the location and a general description of the area set aside for experimental manipulation.

Received September 8, 1970

IN an interim report on pollution in the lower Great Lakes, issued in December 1965, the International Joint Commission (IJC) recommended to the Governments of Canada and the United States that additional support be provided for short-term studies to assess the sources and nature of the pollutants and longer-term research and monitoring programmes to assure the best solutions. Responding to this recommendation in 1966, Canada (under the aegis of the Canadian Section of the IJC and its water pollution boards) established a coordinated and integrated programme of investigations involving three federal departments (Fisheries and Forestry, National Health and Welfare, and Energy, Mines and Resources) and the Ontario Water Resources Commission.

In this coordinated programme, the Department of Fisheries and Forestry through its Fisheries Research Board was assigned responsibility for studies involving biological productivity and for a greater understanding of eutrophication — the important problem of nutrient pollution. To fulfil this responsibility, the Fisheries Research Board created a Eutrophication Section as part of its Freshwater Institute at Winnipeg, Man., with staff also located at the Canada Centre for Inland Waters at Burlington, Ont.

The total programme of the Eutrophication Section includes simultaneous research along four essential lines: (1) assessment of trophic state and mechanisms for the control of cultural eutrophication in the lower Great Lakes themselves; (2) experimental eutrophication studies on small lakes to determine quantitative relations, overall ecological effects, persistence of nutrient pollutants, and remedial measures; (3) comparative studies on trophic conditions in a variety of Canadian lakes to determine the influence of human, climatic, geologic, and morphometric factors on eutrophication; and (4) laboratory studies, toxicity tests, and bioassays using freshwater organisms.

The 14 papers in this issue of the Journal of the Fisheries Research Board of Canada summarize preliminary background information on the general area selected for (2), experimental eutrophication studies on small lakes. This area (see Fig. 1 and the insert map at the back of this issue) has been designated in a generic and regional sense as the Experimental Lakes Area (ELA). Within this larger area with hundreds of small lakes lie 46 small lakes in 17 localized drainage basins (Fig. 1) that, by agreement with the Province of Ontario, have been specifically set aside for experimental research on eutrophication. As the authors of the first paper in this series, our purpose is to summarize the rationale and events that led to the development and realization of this concept of using small lakes.

Why Experimental Lakes?

To appreciate the need for experimental studies on lakes it is necessary to point out certain limitations inherent in observational and laboratory approaches that have provided the bulk of current information on eutrophication. In discussing the eutrophication

[1]The first in a series of 14 papers on the work of the Fisheries Research Board of Canada, describing background environmental data on the Experimental Lakes Area, northwestern Ontario. For location of numbered lakes see insert map at the back of this issue of the Journal of the Fisheries Research Board of Canada. A key to lake locations is given by Cleugh and Hauser (1971).

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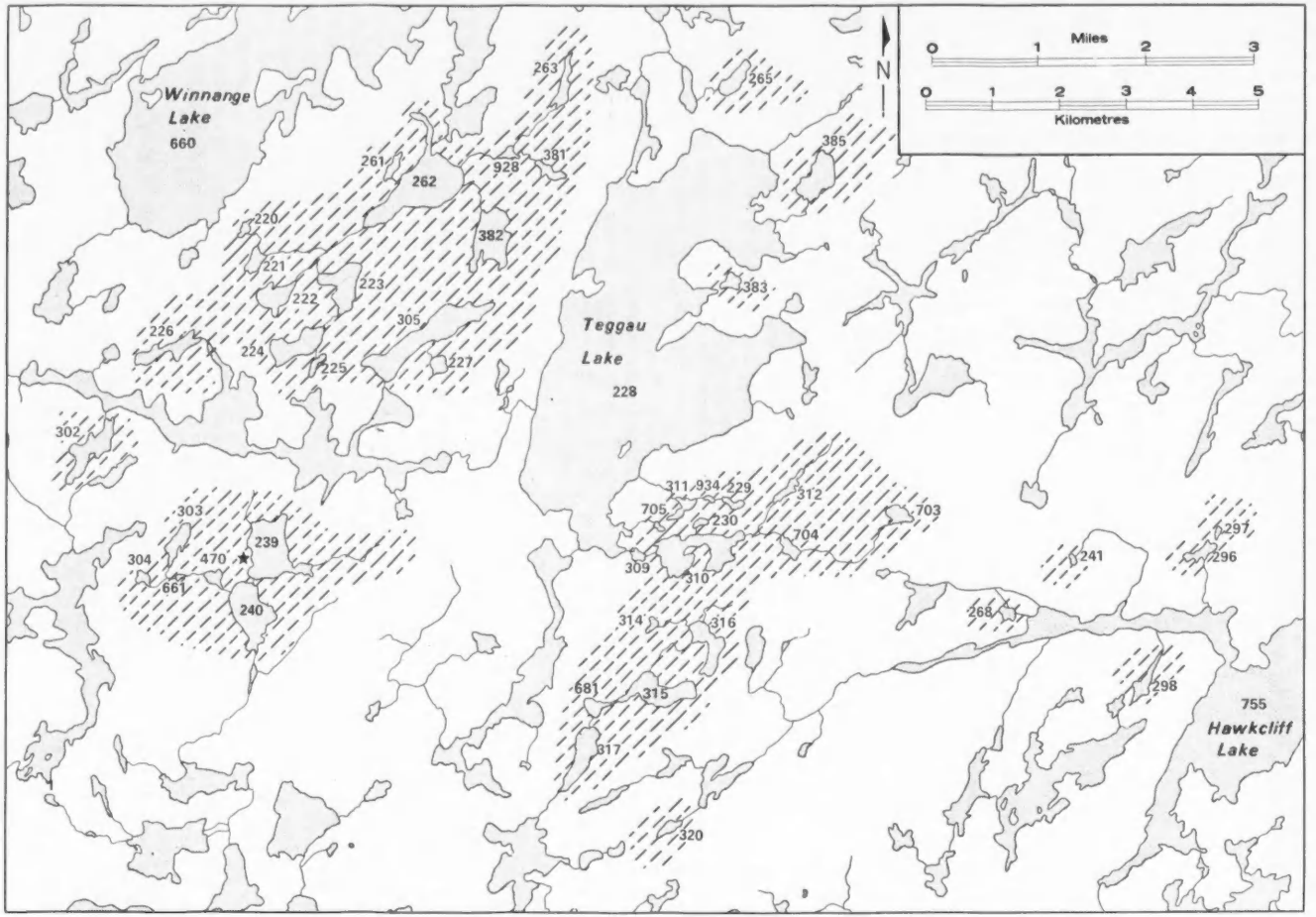

FIG. 1. The central part of the general ELA region showing the 17 drainage basins (hatched areas) including 46 small lakes that have been set aside for research on eutrophication. A star denotes the site of the ELA field station.

problem clear lines of distinction must be drawn between the concepts of cultural eutrophication, natural eutrophication, and the classification of lakes as oligotrophic, mesotrophic, and eutrophic.

Cultural eutrophication is the biological response caused by increased inputs of man-derived nutrients to lakes, i.e., derived from human "culture" in the widest sense of the term. It can be rapid (years to tens of years) in areas of dense population and technological development, and is largely, if not completely, reversible after the elimination of the man-derived nutrient inputs.

Natural eutrophication is the slow biological response produced by the progressive shallowing of lakes as they fill in with sediments over long periods of time. It is a process that requires thousands to tens of thousands of years to produce responses similar to those observed in the past few decades in numerous lakes of the world affected by cultural eutrophication.

The classification of lakes as oligotrophic, mesotrophic, and eutrophic is based on their biological productivity (qualitative and quantitative), but the factors that influence the exact states of the lakes in this respect are diverse. Shallow lakes tend to be more productive per unit volume of surface water than deep lakes; lakes in regions of sedimentary rock drainage tend, because of the leaching of nutrients from the rocks and overlying soils, to be more productive than lakes located in regions of igneous rock drainage; lakes in southerly latitudes tend to be more productive than lakes in high northerly latitudes; and so on. The fact that these differences exist now among natural lakes should not in any way be confused with the changes that have resulted from natural or cultural eutrophication. It is only those mechanisms common to the processes that permit us to apply some of the information derived from one to the other.

Many valuable inferences have been drawn from observational data on both natural and polluted lakes without recourse to premeditated experiment. The text books are full of such examples. In fact, most of our existing knowledge of lakes has been derived from the observation of natural events. On the other hand, observation alone is rarely sufficient for the construction of an exact science, particularly when many variables play interconnected roles in the determination of final states. True appreciation of causes and mechanisms demands freely ranging hypotheses and experimental tests.

Even in the case of unpremeditated "experiments" performed as a result of man-made pollution, it is often difficult if not impossible to disentangle the cause–effect relations because of the simultaneous action of the variety of possible causes and interactions. In Lake Erie, for example, it is impossible to pinpoint the precise causes of changes in the abundance of fish species during the present century due to the interplay of forces associated with selective fishing, overfishing, introduced or invading species, destruction of breeding grounds, eutrophication, and a variety of toxic pollutants.

Laboratory experiments lie at the other end of the spectrum. In such instances more readily manipulated environmental conditions can be varied at will and cause–effect relations established and verified by direct test. Laboratory information, however, applies only to the experimental conditions used, and the fallacy of extrapolating laboratory findings to field conditions has often been demonstrated. Also, many common species of plants and animals cannot at present be cultivated in the laboratory, and in no instance has any reasonably diverse natural community been maintained in the laboratory for an appreciable length of time. In addition, it is often observed that the properties of the organisms cultivated in the laboratory increasingly become a function of the dimensions and properties of the container with the passage of time.

Between the two extremes of observation and study of natural lakes and controlled laboratory experiments lies a continuum that includes aquaria, ponds, and small natural lakes, with progressively less wall effect and greater biological diversity as the dimensions increase. The experimental manipulation of such systems provides a basis of testing for ecological effects and responses with an increasing degree of reliability. In this respect, small natural lakes occupy a position in limnology analogous to that of trial field plots used in agricultural science, or test groups of humans used in medical science, that is, a means of assessing effects on a reduced scale. To deal effectively with such infinitely more complex problems of water pollution as eutrophication, it is obvious that more detailed information on ecosystem responses to environmental modifications is required and that this will only be provided by field tests.

The experimental manipulation of small freshwater ecosystems to determine overall effects has long been studied in connection with the use of manures and artificial fertilizers in fish ponds (DeMoll 1925; Mortimer and Hickling 1954; Maciolek 1954). Juday and Schloemer (1938) were among the first to extend this work to natural lakes in a series of enrichment experiments involving inorganic and organic fertilizer additions to Weber Lake, Wisconsin, during the period 1931–36. Since that time a number of controlled lake enrich-

research on eutrophication. A star denotes the site of the ELA field station.

ment experiments have been performed (e.g., Einsele 1941; Smith 1948, 1969; Langford 1950; Hasler et al. 1951; Nelson and Edmondson 1955; and others). The significance of the experimental lakes concept as developed by the Fisheries Research Board of Canada in its eutrophication studies is thus only new in terms of the extent and systematization of the effort in this direction.

Selection and Development of an Experimental Lakes Area

Efforts to locate a group of small lakes that would be suitable for experimental studies on eutrophication were initiated in 1966. The potential for finding a suitable area in the high-density lake regions of northwestern Ontario and Manitoba was obvious. The criteria used in evaluating possible experimental lake area sites were as follows. (1) The area should be unpopulated and undeveloped, yet reasonably accessible; the lakes and their drainage basins should be free of public and industrial use to avoid uncontrollable effects of man and to minimize interference with costly experiments and scientific equipment. (2) There should be a high density of small lakes of varying mean depth, but including many with well-developed hypolimnia, that is, small enough to permit chemical manipulation at reasonable cost, yet deep enough to possess the thermal stratification patterns characteristic of larger deep lakes. In general, lakes with an area of 1–50 ha and with maximum depths ranging up to more than 20 m were sought. (3) There should be freedom from groundwater influences that might confuse the interpretation of results from defined chemical additions to the lakes. In this regard we followed the guidance of geologists with knowledge of potential areas since time did not permit direct assessment of groundwater influences. (4) It must be possible to obtain exclusive use of certain lakes and their drainage basins for long-term experiments.

The first step in the process was consultation with personnel of agencies familiar with these waters of Manitoba and northwestern Ontario (the Fisheries Branch of the Manitoba Department of Mines and Natural Resources, the Canada Land Inventory Project for Manitoba, and the Ontario Department of Lands and Forests). This was followed by detailed examination of topographic maps and aerial photographs with later survey and exploration by fixed-wing aircraft and helicopter.

By midsummer 1967, it was evident that the best prospect for a suitable experimental lake area was a region in northwestern Ontario east southeast from Kenora. In August 1967, a rental helicopter was fitted with an echo sounder and more detailed rapid examination of 463 lakes in this region was completed in the following weeks. Some of the accumulated data for the lakes examined in this area (lake area, maximum depth, Secchi disc visibility, total dissolved solids, and conductivity) are summarized by Cleugh and Hauser (1971).

This general ELA (see insert map) is located on the Precambrian Shield, approximately 170 miles east of Winnipeg and 35 miles east southeast of Kenora. All of the waters lie in the Winnipeg River drainage, some entering the Winnipeg River via Lake of the Woods, others via the English River. The lakes are composed of relatively low-conductivity waters, and thus are particularly suitable for chemical manipulation in that almost any conceivable chemical environment can be created by controlled additions.

With the cooperation of two logging companies holding timber licences on the area (Dryden Pulp and Paper Company and Ontario–Minnesota Pulp and Paper Company) an agreement with the Ontario Department of Lands and Forests was concluded in April 1968, restricting the use of the 17 desired drainage basins and their 46 lakes (Fig. 1) for experimental research on eutrophication for a period of 20 years, and with a renewal clause for continued use beyond that time. These 46 lakes will serve for a better understanding of cultural eutrophication by experimentation involving controlled additions of various chemical nutrients and the testing of various remedial measures. Other lakes in the surrounding larger ELA are being studied in their natural condition for comparative purposes.

To provide the necessary field laboratory and living facilities for work in ELA, a series of specially designed trailers were purchased. Several of these were moved to a site at lake 132, which had road access, to provide temporary field facilities during the summer of 1968. The site selected for the permanent field station was in one of the 17 basins set aside for experimental research — at the junction of lakes 239 and 240 (Fig. 1). Construction of a 4.1-mile access road to this site was completed in November 1968; necessary electrical, water, and sewage systems were installed and the trailers established on the permanent site soon after. A series of access trails to lakes in the other 17 experimental basins was completed during the summer of 1969. The first whole lake enrichment experiment was initiated in June 1969. By the summer of 1970, well-equipped field living and laboratory accommodation was available for up to 32 investigators on a year-round basis.

In addition to the Fisheries Research Board of Canada several other agencies have played a major

role in the development of ELA facilities and research: the University of Manitoba, on studies of surface and subsurface hydrology through contract support from the Department of Energy, Mines and Resources (DEMR); the Winnipeg office of the Water Survey of Canada (DEMR), on measurement of lake levels and stream flow; the Winnipeg office of the Meteorological Branch, Department of Transport, on meteorological measurements; and the Lakes Division of the Canada Centre for Inland Waters (DEMR), on physical interactions at the air–water interface and general hydrology.

Experimental Lakes to Other Lakes Information Transfer from

The ELA waters under study are located on the Canadian Precambrian Shield and in that respect are probably fairly typical of lakes in the vast region of igneous rock drainage that occupies half of the land surface of Canada and contains the majority of Canadian lakes. This in itself is an important consideration, for our knowledge of these lakes is meager. Detailed extrapolation obviously cannot be made to lakes in regions of sedimentary rock drainage; comparative study of lakes in regions of sedimentary rock drainage is an obvious necessity. Many ELA lakes are of a mixotrophic character, i.e., intermediate between lakes of the "harmonic" series and dystrophic lakes. This must be considered, where pertinent, in extrapolating information to lakes elsewhere.

An even more important question that might be asked is the extent to which information derived from small lakes can be transferred to larger bodies of water. Two answers can be given. The first and most direct is that the extent of valid information transfer is far better from small natural lakes to large lakes than from test tubes to large lakes (i.e., there really is no choice). The second answer is that differences do come into play and must be taken into account in any extrapolation. For example, in small lakes the area of the littoral zone tends to be accentuated, the volume ratio of epilimnion to hypolimnion tends to be high, and chemicals added at a point source tend to be more effectively distributed throughout small lakes in shorter times than would ever be the case in large bodies of water such as the St. Lawrence Great Lakes. Also, because of protection from the wind, surface turbulence and the depth of the epilimnion are less than in large lakes. For all these reasons care must be taken in the extrapolation of information from one situation to the other, but the problems are not any more complex than in comparing similar lakes in different watersheds, or otherwise identical lakes that have varying water replenishment times, mineral turbidity, or sedimentation rates.

Regarding the problem of cultural eutrophication, the fact that lakes of a great range of types and sizes in various parts of the world have responded similarly to nutrient pollution lends support to the view that significant contributions to a fundamental understanding of this general problem can emerge from detailed study and experimentation on these small lakes.

Canada occupies an enviable position in respect to the availability of small unused lakes for experimental purposes. With the increasing degree of complexity of water pollution problems in our modern society, the need for controlled studies in areas free from public and industrial interferences increases. There is every reason to believe that the use of small isolated lakes for experimental purposes will immeasurably enhance our knowledge of lakes and the efficacy of specific pollution abatement measures.

Acknowledgments

Mr K. Irizawa and the staff of the Kenora District Office of the Ontario Department of Lands and Forests were particularly helpful in bringing this experimental lakes program to fruition. We are indebted to the Ontario–Minnesota and Dryden Pulp and Paper companies for their readiness in relinquishing logging rights to areas within the boundaries of their timber licence areas. Mr P. W. Strilaeff of the Water Survey of Canada (DEMR), Mr D. W. Robertson of the Meteorological Branch of the Department of Transport, and Dr R. A. Lane of Lakes Division (DEMR) of the Canada Centre for Inland Waters were most helpful in facilitating arrangements for physical studies. The procurement and installation of field facilities resulted from the combined efforts of Messrs C. G. Jones, H. Schneider, S. E. Schick, T. R. Cleugh, and others involved in both construction and administrative aspects. The authors of all the papers express their thanks to Mrs G. Porth for patience, care, and efficiency in the typing of the manuscripts. The extent to which Dr D. W. Schindler has participated in all aspects of the project will be apparent from the results of the work reported in this issue of the Journal of the Fisheries Research Board of Canada.

CLEUGH, T. R., AND B. W. HAUSER. 1971. Results of the initial survey of the Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Bd. Canada 28: 129–137.

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Results of the Initial Survey of the Experimental Lakes Area, Northwestern Ontario[1]

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CLEUGH, T. R., AND B. W. HAUSER. 1971. Results of the initial survey of the Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Bd. Canada 28: 129–137.

A reference list is given to locations, areas, maximum depths, transparencies, total dissolved solids, and conductivities of lakes shown on the insert map of the Experimental Lakes Area in the back of this issue.

Received September 25, 1970

THIS article summarizes information obtained from a rapid helicopter survey of 463 lakes located in the Experimental Lakes Area (ELA), northwestern Ontario, during the autumn of 1967 (Table 1). In addition, the coordinates are listed for the location of all of the 1004 numbered lakes shown on the insert map at the back of this issue of the Journal of the Fisheries Research Board of Canada. Reasons for the selection of this area as a study site and the location of 46 lakes specifically designated for eutrophication research are given by Johnson and Vallentyne (1971). Descriptions and more complete limnological data on some of the lakes are given in other papers of this series, all included in this issue.

The lakes shown on the insert map (see inside-back cover) were numbered consecutively in the order in which they were sampled, all in 1967. Lakes 1–86 were sampled from September 11 to 16; lakes 87–197 from September 18 to 22; lakes 198–268 from September 25 to 29; lakes 269–391 from October 2 to 6; and lakes 392–463 from October 17 to 19. Lakes 464–1004 were not sampled but were numbered to facilitate ready identification in future studies. Lakes 449–457 are located north of Highway 17 and, for arbitrary reasons, were not included on the map.

The areas of the lakes were determined planimetrically from aerial photographs taken during the autumn of 1952. The insert map is based on aerial photographs taken in the autumn of 1965 at an altitude of 1320 ft.

Maximum depths were determined using a recording echo sounder attached to the frame of the helicopter. On small lakes the usual procedure was to traverse the long axis of the lake; on larger multibasin lakes sounding was done at several points. Secchi disc visibility was measured and a 500-ml sample of water taken just below the surface at the position of maximum depth. The unfiltered water samples were returned to the laboratory where they were analyzed for total dissolved solids and specific conductivity. Total dissolved solids were determined by evaporating 100 ml of a filtered sample in a tared evaporating dish under an infrared lamp until just dry. The samples were then dried in an oven at 110 C for 1 hr, cooled in a desiccator, and weighed. Results are reported to the nearest 10 mg/liter. Specific conductivity in micromhos was determined at 25 C in a water bath using 0.01 N KCl as a reference solution, rinsing the electrode in one portion of the sample prior to measurement in a second portion.

Figure 1 shows histograms of maximum depth and Secchi disc visibility for the 463 lakes examined.

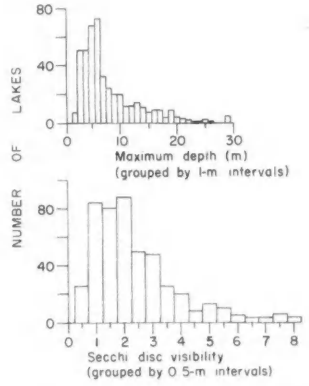

FIG. 1. Frequency histograms of maximum depth and Secchi disc visibility for the 463 ELA lakes examined.

[1]The second in a series of 14 papers on the work of the Fisheries Research Board of Canada, describing background environmental data on the Experimental Lakes Area, northwestern Ontario. For location of numbered lakes see insert map at the back of this issue of the Journal of the Fisheries Research Board of Canada. A key to lake locations is given in this paper.

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TABLE 1. Characteristics and map coordinates of 1004 lakes in the Experimental Lakes Area (ELA), northwestern Ontario. Abbreviations: A_o, surface area (hectares); z_m, maximum depth (meters); SDV, Secchi disc visibility (meters); TDS, total dissolved solids (milligrams/liter); C, conductivity (micromhos/centimeter at 25 C); *, indicates lakes that are not shown on the ELA map; +, indicates lakes that are controlled by the Freshwater Institute, Fisheries Research Board of Canada; shallow, indicates less than 1 m in depth.

Lake	Location	A_o	z_m	SDV	TDS	C	Lake	Location	A_o	z_m	SDV	TDS	C
1	AS	6.2	6.7	2.0	30	20	51	AW	19.0	10.6	2.5	50	57
2	AS	13.9	3.3	1.5	30	18	52	AW	3.6	1.5	0.75	80	46
3	AT	5.2	6.1	2.0	70	19	53	AX	26.4	3.6	1.7	90	115
4	AT	1.0	6.1	0.7	90	22	54	DX	8.9	2.7	1.0	50	27
5	AT	1.5	3.3	0.5	100	37	55	CX	3.9	8.5	1.7	20	18
6	AT	16.2	3.9	1.2	60	23	56	CX	24.3	5.4	1.0	50	37
7	BT	9.1	3.0	0.8	80	28	57	BX	3.7	7.3	2.5	70	117
8	BU	3.2	12.2	7.0	40	18	58	BX	10.2	1.5	1.5	80	75
9	BU	8.6	3.9	0.8	90	58	59	BX	10.7	2.7	2.0	70	114
10	AU	1.1	3.0	0.9	80	30	60	CW	6.5	1.8	1.8	60	98
11	BT	7.5	4.5	1.0	70	34	61	CW	6.0	4.8	2.0	20	16
12	BT	4.2	2.5	1.0	60	34	62	DU	10.9	4.2	1.0	30	24
13	AU	13.6	5.4	1.2	80	74	63	DT	13.9	8.2	3.0	30	29
14	AV	19.8	19.7	2.0	60	79	64	DU	10.0	3.0	1.5	20	20
15	AV	10.2	9.4	1.5	70	84	65	CU	2.8	4.2	1.0	50	18
16	AV	4.5	4.2	1.5	60	66	66	CT	4.5	5.7	1.5	30	18
17	AV	25.9	13.4	2.0	90	100	67	CT	15.1	10.8	2.0	20	22
18	AV	11.5	9.7	3.5	100	161	68	BS	4.7	4.8	1.25	30	32
19a	BV	6.8					69	CT	15.7	7.3	1.0	30	27
19	BW	3.4	6.8	2.0	50	69	70	CT	11.0	3.5	0.5	30	38
20	BV	3.6	5.4	2.0	60	73	71	CS	6.0	2.1	1.0	50	30
21	AV	1.9	4.2	2.0	80	99	72	CS	1.8	1.8	1.0	40	37
22	AV	8.7	6.7	0.5	90	133	73	CS	13.6	3.6	2.0	32	20
23	AW	8.1	5.4	1.5	30	39	74	DS	1.0	4.8	1.0	34	18
24	AW	2.6	3.0	1.0	30	48	75	DR	6.6	5.7	3.0	24	19
25	AW	1.3	2.4	1.5	40	38	76	DS	4.1	3.0	1.0	59	28
26	AW	15.1	9.1	2.5	20	27	77	ES	3.2	2.7	1.5	28	15
27	AW	23.0	3.3	1.5	20	23	78	ES	8.4	2.4	1.5	33	19
28	AW	10.7	5.4	1.5	20	24	79	ES	4.4	4.8	1.5	36	18
29	AX	8.6	9.1	1.5	30	25	80	ET	9.2	7.9	4.0	16	20
30	AW	10.4	10.6	1.5	20	27	81	CU	1.3	7.0	2.0	35	24
31	AX	3.7	4.2	0.7	50	18	82	DU	9.9	4.0	1.0	63	50
32	AT	18.1	9.7	2.0	30	20	83	CV	6.0	1.5	0.25	27	25
33	BT	1.3	4.2	0.7	40	26	84	CV	9.9	9.4	2.0	58	70
34	BU	4.9	4.2	1.0	20	35	85	DV	1.8	3.3	2.0	12	25
35	BU	13.3	9.1	1.5	40	46	86	DV	11.7	7.0	2.5	19	21
36	BU	4.2	15.2	1.5	70	72	87	ES	9.9	3.0	1.0	62	38
37	BU	1.6	7.6	1.0	60	57	88	ER	7.5	9.7	2.5	7	16
38	BU	4.2	2.4	1.5	40	25	89	ES	3.1	14.0	2.0	26	20
39	BU	18.5	2.4	0.8	40	42	90	ER	18.5	12.8	1.5	28	22
40	BU	15.0	13.7	1.7	40	37	91	FS	3.7	2.4	2.4	15	16
41	BU	2.3	4.5	1.5	40	45	92	FS	19.7	2.4	1.5	30	22
42	BV	6.2	3.0	0.5	80	104	93	GS	7.9	10.3	3.0	16	18
43	BV	5.5	16.4	0.75	80	99	94	FT	3.7	2.4	2.4	19	21
44	BV	5.7	3.0	3.0	30	78	95	FT	3.7	7.6	1.0	38	22
45	CV	8.6	2.1	2.1	20	55	96	FT	1.9	1.5	0.5	85	19
46	BV	9.7	4.8	2.0	40	65	97	FS	4.2	4.8	1.5	25	24
47	BW	2.1	4.8	0.75	50	34	98	GS	9.2	1.5	1.5	26	28
48	BW	5.3	5.7	1.5	40	34	99	GS	6.5	7.6	2.0	15	20
49	BW	22.7	2.1	1.5	40	36	100	GT	11.1	12.8	3.0	10	25
50	BW	22.5	15.2	3.0	50	69	101	GT	10.0	Shallow			

(*Continued*)

TABLE 1. Characteristics and map coordinates of 1004 lakes in the Experimental Lakes Area (ELA), northwestern Ontario. Abbreviations: A_o, surface area (hectares); z_m, maximum depth (meters); SDV, Secchi disc visibility (meters); TDS, total dissolved solids (milligrams/liter); C, conductivity (micromhos/centimeter at 25 C); *, indicates lakes that are not shown on the ELA map; +, indicates lakes that are controlled by the Freshwater Institute, Fisheries Research Board of Canada; shallow, indicates less than 1 m in depth.

Lake	Location	A_o	z_m	SDV	TDS	C	Lake	Location	A_o	z_m	SDV	TDS	C
102	GT	5.3	2.4	2.0	18	21	153	ET	4.5	8.5	1.5	40	18
103	GT	2.3	4.2	2.0	5	18	154	EU	17.8	10.3	3.0	10	19
104	GT	8.1	4.8	2.0	18	21	155	ET	6.0	0.9	0.5	80	83
105	GT	6.2	2.4	1.5	5	18	156	DT	28.5	8.2	2.0	50	42
106	HS	3.7	2.4	1.5	51	57	157	CV	25.7	7.9	2.5	60	96
107	HS	5.0	7.0	1.0	8	21	158	CV	3.9	8.8	1.5	80	103
108	GS	9.1	3.3	2.0	20	34	159	CV	36.3	7.3	2.5	50	39
109	GS	14.6	9.7	4.0	10	20	160	CV	21.1	18.2	4.0	40	47
110	GS	6.3	15.2	3.0	7	15	161	FU	1007	>117	>6.0	20	28
111	GS	9.9	>30.0	4.0	13	18	162	FU	4.2	3.8	1.8	40	23
112	HT	6.8	2.1	2.1	36	16	163	GU	15.7	8.5	3.5	40	28
113	HT	4.5	1.5	1.5	12	27	164	GV	15.3	6.6	3.0	50	21
114	HT	12.1	5.0	2.5	9	17	165	GU	11.4	4.8	2.0	30	22
115	HT	6.5	1.5	1.5	18	19	166	GU	2.1	5.4	0.8	60	16
116	GT	0.8	2.0	2.0	62	13	167	HU	2.1	6.4	2.0	40	18
117	GT	6.5	3.0	1.5	6	15	168	HU	5.8	6.7	3.0	30	19
118	GT	2.3	1.0	1.0	11	13	169	HV	2.3	4.2	2.0	50	20
119	GU	8.7	2.4	1.5	15	23	170	GV	2.6	5.7	1.6	30	18
120	GU	9.3	19.0	>7.0	8	17	171	GV	5.5	4.2	2.0	30	20
121	FU	3.4	2.4	2.0	34	17	172	FV	27.1	12.2	3.5	50	25
122	FU	12.2	12.8	3.5	35	16	173	GV	13.4	5.4	3.0	40	25
123	FU	2.9	6.1	2.0	35	16	174	EV	12.2	6.1	2.0	20	19
124	FU	11.3	20.6	5.0	41	21	175	CV	9.4	11.5	5.0	20	23
125	FU	2.9	9.1	1.5	31	17	176	CV	9.7	3.6	0.7	10	56
126	FU	1.6	3.6	2.5	25	14	177	CV	7.9	5.4	1.0	40	23
127	FU	4.7	5.2	2.0	23	16	178	CW	0.8	3.0	1.8	20	17
128	GU	8.1	2.4	1.5	30	20	179	CW	1.1	6.1	2.5	20	14
129	GU	4.5	5.4	2.0	4	20	180	DW	15.1	10.3	2.0	30	19
130	GU	7.6	5.7	2.5	27	16	181	DW	7.0	3.3	0.8	60	29
131	GU	3.1	2.4	2.4	24	15	182	DW	2.9	4.8	1.0	60	35
132	FU	7.2	8.4	2.5	14	14	183	DX	5.3	4.2	1.6	40	24
133	GU	3.7	3.3	1.5	13	14	184	IV					
134	FT	4.1	2.4	2.0	19	19	185	DW	8.1	2.4	2.4	10	25
135	FU	12.5	7.0	3.0	25	20	186	DW	4.2	5.4	1.0	20	21
136	EU	2.6	8.5	1.5	30	19	187	GV	4.5	8.5	3.0	10	16
137	EU	12.8	8.5	4.0	22	30	188	GV	36.6	>25.0	6.0	20	19
138	EV	29.6	3.0	1.5	22	32	189	GV	28.8	15.8	6.0	30	22
139	ET	3.7	2.4	2.4	10	26	190	HV	4.9	6.1	3.0	60	25
140	EU	10.5	9.1	1.5	20	17	191	HW	19.4	4.2	1.2	50	28
141	EU	3.4	4.2	2.0	3	13	192	GW	10.7	3.6	2.5	30	19
142	AS	9.4	4.8	2.0	9	31	193	HW	1.9	5.4	1.2	40	12
143	AS	10.0	6.2	2.0	18	19	194	FW	5.7	4.8	2.3	20	20
144	CS	4.4	7.3	3.5	15	22	195	FW	1.0	4.5	1.2	40	21
145	CS	0.6	5.4	1.5	10	18	196	EW	2.1	4.8	0.9	60	25
146	DS	9.7	7.0	4.0	20	32	197	EW	4.5	1.5	0.6	80	32
147	DS	8.3	1.2	1.2	20	27	198	FX	3.6	2.5	0.5	70	38
148	DS		18.2	5.0	10	33	199	DW	13.6	3.9	2.0	20	27
149	ET	28.0	4.2	3.0	10	29	200	DW	3.4	4.2	1.0	30	21
150	ET	11.8	7.3	1.5	20	33	201	DW	4.9	4.5	0.5	40	20
151	ET	6.5	4.2	1.5	10	20	202	DW	4.7	6.0	2.0	10	35
152	ET	5.3	6.1	2.5	10	26	203	DW	4.1	3.6	1.5	20	24

(*Continued*)

TABLE 1. Characteristics and map coordinates of 1004 lakes in the Experimental Lakes Area (ELA), northwestern Ontario. Abbreviations: A_o, surface area (hectares); z_m, maximum depth (meters); SDV, Secchi disc visibility (meters); TDS, total dissolved solids (milligrams/liter); C, conductivity (micromhos/centimeter at 25 C); *, indicates lakes that are not shown on the ELA map; +, indicates lakes that are controlled by the Freshwater Institute, Fisheries Research Board of Canada; shallow, indicates less than 1 m in depth.

Lake	Location	A_o	z_m	SDV	TDS	C
204	DV	10.5	15.2	4.0	10	20
205	EV	13.4	3.3	2.0	30	32
206	EV	10.7	16.4	3.0	20	25
207	EV	7.0	10.9	4.0	40	25
208	DU	9.7	14.9	4.0	40	31
209	DU	2.6	5.1	2.0	20	18
210	DV	5.8	7.3	2.0	30	23
211	DU	33.4	2.4	2.4	20	23
212	DV	4.4	8.2	2.0	30	19
213	DV	17.5	15.2	3.5	20	30
214	DU	15.9	17.0	4.0	30	62
215	DU	16.2	1.8	1.5	30	75
216	DT	7.0	5.4	2.0	20	22
217	DT	2.6	7.3	2.0	10	18
218	GT	2.3	3.9	2.0	30	14
219	HT	6.4	2.4	2.4	20	20
220+	HT	4.2	3.3	3.3	30	19
221+	HT	8.9	5.4	3.0	20	21
222+	HT	17.5	5.4	2.2	30	32
223+	IT	30.2	11.2	5.0	40	23
224+	HT	25.4	16.7	7.0	40	18
225+	IT	5.6	1.8	1.7	50	17
226+	HT	21.8	12.2	4.2	40	17
227+	IT	5.0	10.0	2.6	60	21
228	IT	1330		>10.0	30	23
229+	JT	3.1	3.6	2.9	40	19
230+	JT	1.7	13.6	5.1	40	15
231	IU	3.4	2.4	1.1	10	20
232	IU	7.6	1.6	1.2	30	25
233	IV	2.8	6.1	1.0	20	19
234	IV	1.5	6.1	1.2	10	18
235	IV	2.8	8.2	1.2	10	15
236	IV	9.6	8.2	2.1	10	16
237	JV	7.5	4.8	1.6	10	14
238	JV	4.2	3.9	3.5	10	11
239+	HU	56.1	30.4	4.8	20	25
240+	HU	44.1	13.1	4.2	20	22
241+	KU	1.8	12.5	2.5	10	18
242	LT	7.0	3.6	2.6	20	23
243	LT	7.3	4.2	1.7	60	19
244	LT	6.0	5.1	3.5	40	19
245	LS	14.4	4.5	2.6	30	25
246	MU	2.8	6.7	1.6	60	22
247	MU	0.8	3.6	0.8	70	25
248	MU	6.5	5.4	1.4	20	20
249	DT	1014	21.2	5.3	70	32
250	DT	50.8	5.4	3.1	70	35
251	DT	100	17.3	6.3	90	34
252	CT	35.3	9.7	2.7	70	59
253	CS	33.5	3.6	2.4	50	26
254	ET	388	>30.0	7.6	60	32
255	ET	32.4	15.8	3.7	30	20
256	FT	120	22.4	7.8	30	24
257	GT	28.2	7.6	2.6	20	18
258	GT	73.2	>30.0	3.9	30	18
259	GT	96.9	20.3	6.3	30	18
260	HT	32.4	14.6	4.9	20	20
261+	IS	5.6	9.6	3.0	30	16
262+	IS	84.2	>30.0	5.3	30	23
263+	IS	9.3	4.8	3.2	20	14
264	IS	8.4	2.4	1.8	20	15
265+	JS	13.1	18.6	4.5	30	15
266	JS	21.2	6.1	3.2	20	21
267	KS	12.8	1.8			
268+	KU	4.4	14.6	5.1	40	24
269	HV	4.9	4.2	1.7	40	40
270	IW	0.8	9.1	0.8	70	41
271	IW	38.9	5.4	2.0	40	31
272	IW	43.7	28.3	4.0	40	28
273	IW	7.3	8.2	2.2	40	21
274	IV	28.0	4.5	2.5	20	18
275	IW	64.2	18.2	4.0	50	29
276	IW	13.9	7.3	1.2	30	25
277	IX	11.7	15.2	2.2	30	27
278	IX	9.1	5.7	1.5	50	29
279	IX	16.5	11.2	3.0	40	24
280	IX	22.0	19.1	6.2	30	27
281	IX	16.2	4.8	2.2	40	34
282	IX	29.8	17.3	3.5	40	29
283	IW	8.4	8.5	2.5	30	30
284	IW	12.2	5.1	1.2	80	26
285	IW	11.5	3.0	1.2	80	24
286	JW	27.7	12.2	1.8	40	25
287	IX	29.5	17.9	5.0	30	29
288	IX	17.0	7.9	1.7	30	41
289	IX	7.8	3.0	2.0	40	35
290	IX	23.2	13.4	2.0	50	36
291	IX	8.9	2.7	1.0	60	41
292	IX	5.5	6.7	2.3	40	44
293	IX	6.7	2.4	0.5	110	67
294	JX	1.6	5.4	0.7	90	23
295	JW	6.8	2.4	2.4	60	20
296+	KU	6.0	8.2	3.0	60	20
297+	KT	1.5	2.4	1.6	80	22
298+	KU	7.6	16.1	4.0	50	19
299	KU	3.2	3.9	3.0	70	18
300	KU	5.5	3.3	2.7	60	21
301	KR	118	14.6	5.0	50	21
302+	HT	23.7	13.8	2.8	50	19
303+	HU	9.9	2.5	2.5	50	17
304+	HU	3.6	6.7	1.9	40	16
305+	IT	52.0	32.7	8.0	20	24

(*Continued*)

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Lake	Location	A_o	z_m	SDV	TDS	C	Lake	Location	A_o	z_m	SDV	TDS	C
306	IT	2.8	4.2	1.7	10	24	357	NW	6.8	3.6	1.0	30	38
307	IT	2.8	2.4	1.3	20	21	358	NW	8.1	3.9	1.5	20	24
308	IU	20.8	24.4	3.3	20	22	359	OW	6.5	5.4	1.0	40	31
309+	JU	2.6	1.8	1.4	20	28	360	OW	13.0	4.2	2.0	10	29
310+	JU	49.7	>19.7	2.7	40	23	361	OW	3.1	5.7	1.0	20	22
311+	JT	5.7	11.9	3.5	10	20	362	OW	4.1	3.9	1.0	20	23
312+	JT	6.8	4.8	1.0	20	25	363	OW	3.4	5.1	1.0	10	25
313	IU	114	24.4	2.5	20	21	364	OW	11.0	3.9	1.0	20	23
314+	JU	1.9	9.4	2.7			365	OX	4.7	5.1	1.5	10	23
315+	JU	32.7	>12.8	3.8	20	24	366	NX	2.6	1.2	0.5	40	26
316+	JU	20.1	5.1	2.0	30	20	367	OX	1.6	3.0	0.5	40	22
317+	IU	25.6	18.8	3.0	40	21	368	OX	1.1	4.8	0.5	30	19
318	IU	6.0	3.6	1.7	30	17	369	OX	4.9	3.6	3.0	30	41
319	IV		4.8	2.5	40	19	370	NX	1.8	5.4	2.0	10	22
320+	JU	4.5	17.3	3.3	30	17	371	NX	1.9	4.2	1.0	40	27
321	IV		4.2	1.7	30	18	372	MX	7.3	5.7	4.5	20	24
322	IV	74.1	18.8	3.7	30	21	373	GS	28.3	>16.4	7.5	20	26
323	LV	8.3					374	GS	485	>30.0	5.0	30	27
324	LV	5.7	14.0	4.0	20	41	375	GS	22.3	>19.4	5.5	40	46
325	LV	6.2	7.3	3.0	10	27	376	HR	711	>16.4	5.5	20	31
326	LV	2.8	3.3	1.0	10	22	377	HS	27.2	>12.8	4.5	10	23
327	LV	1.3	5.1	1.0	10	22	378	HS	25.9	11.5	4.5	30	20
328	LV	3.3	2.7	2.0	10	17	379	GS	166	26.7	5.5	20	23
329	LV		6.7	2.0	20	15	380	IS	29.0	>10.9	4.5	30	27
330	LV	6.5	2.2	2.0	30	22	381+	IS	6.0	3.3	2.0	30	19
331	MV	1.0	2.4		50	31	382+	IT	37.3	11.9	3.0	20	21
332	MV	2.4	6.1	1.0	40	33	383+	JT	5.2	9.4	3.5	30	24
333	LW	8.6	6.1	1.0	20	35	384	JT	6.3	3.3	2.5	20	18
334	LW	6.3	3.9	1.0	40	43	385+	JS	24.9	14.0	5.0	20	18
335	LV	7.3	4.8	1.3	50	49	386	JS	2.3	5.1	2.5	30	19
336	LV	8.4	12.2	3.0	120	49	387	JS	8.1	7.6	2.0	20	17
337	LW	22.7	10.9	3.0	110	54	388	JS	29.6	>18.2	3.5	20	33
338	LW	10.8	7.9	3.0	120	55	389	KS	9.5	4.2	3.0	30	19
339	LW	6.2	5.6	1.0	110	53	390	KS	3.4	5.1	3.0	30*	21
340	LW	10.4	5.1	1.0	140	67	391	KS	11.8	4.8	2.5	30	21
341	LW	7.3	5.4	1.0	110	83	392	CR	6.3	10.0	1.5	20	51
342	LW	5.0	4.2	2.0	110	57	393	CR	4.9	2.0	1.5	20	57
343	LW	1.8	4.2	2.0	110	75	394	DQ	8.9	7.0	3.0	20	27
344	MW	2.3	2.7	1.0	110	27	395	DQ	2.9	18.0	4.5	10	21
345	MW	1.5	5.1	1.0	110	19	396	DR	1.9	5.0	3.0	20	19
346	MW	2.6	5.7	1.0	60	19	397	KT					
347	MW	21.1	5.7	1.0	60	40	398	ER	28.5	13.0	3.0	30	21
348	MW	9.1	2.4	1.0	20	30	399	ER	8.1	5.0	2.5	40	20
349	NW	10.4	5.4	1.0	40	29	400	ER	5.7	10.0	2.0	20	21
350	NW	7.0	2.4	1.0	40	29	401	ER	0.8	5.0	1.5	10	17
351	NV	4.9	12.5	1.0	40	32	402	ER	5.0	14.0	4.5	20	18
352	MV	6.0	1.8	1.0	60	28	403	ER	11.7	8.0	3.5	10	22
353	MV	0.8	4.5	1.0	50	31	404	EQ	6.5	3.0	2.0	20	45
354	NV	1.1	4.5	1.0	70	52	405	EQ	6.6	1.0	1.0	30	24
355	NV	3.2	4.8	2.0	20	39	406	EQ	11.0	5.0	2.5	10	25
356	OV	12.5	7.0	2.0	30	37	407	EQ	6.6	2.0	1.5	20	32

(*Continued*)

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Lake	Location	A_o	z_m	SDV	TDS	C	Lake	Location	A_o	z_m	SDV	TDS	C
408	DQ	8.3	3.0	2.5	20	33	436	GR	8.6	5.0	2.5	30	18
409	DQ	1.6	2.0	1.0	30	26	437	GR	10.0	1.2	1.2	40	19
410	ER	1.0	4.0	2.0	10	18	438	GR	17.0	4.0	2.0	40	17
411	ER	8.4	4.0	2.5	20	27	439	GQ	0.8	2.0	2.0	10	20
412	ER	11.5	9.0	2.5	4	22	440	GR	8.9		1.6	4	31
413	ER	19.8	14.5	5.5	20	21	441	GR	5.3	3.0	1.5	10	21
414	EQ	8.3	1.5	1.5	10	33	442	GR	15.6	12.0	4.2	20	24
415	EQ	2.1	1.5	1.5	30	20	443	GR	8.4	6.0	2.0	10	17
416	EQ	4.5	1.7	1.7	30	17	444	GR	1.5	4.7	4.7	20	16
417	FQ	15.9	5.5	5.2	20	19	445	FR	2.1				
418	FQ	2.4	3.0	1.5	10	18	446	FR	1.5	4.0	2.3	10	11
419	FQ	2.1	3.0	2.0	10	17	447	FR	7.3	2.0	1.0	20	24
420	FQ	1.5	8.0	3.0	10	18	448	FR	6.8	1.8	1.8	5	17
421	HR	17.0	12.0	2.5	10	22	449	*		4.0	0.8	30	23
422	HR	0.3	3.5	0.7	30	16	450	*		3.0	1.0	40	24
423	IR	1.8	3.5	0.8	20	19	451	*		5.5	2.2	70	23
424	IR	5.8	8.0	1.5	50	22	452	*		4.0	3.5	10	54
425	IR	23.3	6.0	3.5	20	36	453	*		4.0	1.7	40	24
426	HQ	1.6	3.5	1.0	80	20	454	*		5.0	2.0	30	20
427	HQ	10.0	3.0	3.0	20	20	455	*		5.0	3.0	20	20
428	HR	6.0	12.0	3.5			456	*		3.3	1.8	30	20
429	HR	16.0	5.5	2.5	30	25	457	*		4.0	1.2	30	16
430	HR	14.3	5.0	2.0	30	24	458	FQ	2.6	3.0	2.0	20	26
431	HR	0.6	4.0	0.7	50	20	459	FQ	8.6	1.5	1.2	40	21
432	HR	9.2	3.5	3.5	30	19	460	FQ	4.7	4.0	1.8	40	32
433	HQ	5.7	5.0	1.7	20	17	461	FR	8.1	1.3	1.3	40	34
434	GQ	8.6	4.0	2.0	30	19	462	FR	20.6	1.3	1.0	60	59
435	GQ	5.7	2.4	2.4	20	19	463	FR	13.3	5.0	2.5	40	32

Lake	Location	Lake	Location	Lake	Location	Lake	Location
464	FS	483	AW	502	BW	521	CU
465	GV	484	AW,	503	BW	522	CU
466	GX	485	AX	504	BW	523	CU
467	HU	486	AX	505	AX	524	CU
468	HT	487	AX	506	BX	525	CU
469	NQ	488	AX	507	BX	526	BW
470+	HU	489	AX	508	BX	527	CW
471	AR	490	BR	509	BX	528	CX
472	AR	491	BR	510	BX	529	DQ
473	AR	492	BR	511	CR	530	DR
474	AS	493	BR	512	CR	531	DR
475	BS	494	BR	513	CR	532	DR
476	AT	495	BU	514	CR	533	DR
477	AU	496	BU	515	CR	534	DR
478	AV	497	AV	516	CR	535	DR
479	AV	498	BV	517	CR	536	DR
480	AV	499	BV	518	CS	537	DS
481	AW	500	BV	519	CS	538	DS
482	AW	501	BV	520	CU	539	DS

(*Continued*)

TABLE 1. Characteristics and map coordinates of 1004 lakes in the Experimental Lakes Area (ELA), northwestern Ontario. Abbreviations: A_o, surface area (hectares); z_m, maximum depth (meters); SDV, Secchi disc visibility (meters); TDS, total dissolved solids (milligrams/liter); C, conductivity (micromhos/centimeter at 25 C); *, indicates lakes that are not shown on the ELA map; +, indicates lakes that are controlled by the Freshwater Institute, Fisheries Research Board of Canada; shallow, indicates less than 1 m in depth.

Lake	Location	Lake	Location	Lake	Location	Lake	Location
540	DU	592	FR	644	HQ	696	JT
541	DU	593	FR	645	HQ	697	JT
542	DU	594	FR	646	HQ	698	JT
543	DU	595	FT	647	HQ	699	JX
544	DV	596	FT	648	HQ	700	GU
545	DV	597	FW	649	HQ	701	JT
546	DV	598	FW	650	HQ	702	JT
547	DV	599	FW	651	HQ	703+	JT
548	DW	600	GP	652	GQ	704+	JU
549	DW	601	GQ	653	HR	705+	JT
550	DW	602	GP	654	HR	706	JU
551	DW	603	GQ	655	HR	707	JU
552	DX	604	GQ	656	HR	708	JU
553	DX	605	GQ	657	HS	709	JU
554	DX	606	GQ	658	HS	710	JU
555	DX	607	GP	659	HS	711	JU
556	EQ	608	GQ	660	HS	712	JU
557	EQ	609	GP	661+	HU	713	JU
558	EQ	610	GP	662	HU	714	JV
559	EQ	611	GQ	663	HU	715	JV
560	EQ	612	GQ	664	HV	716	JV
561	ER	613	GQ	665	GU	717	JV
562	EQ	614	GQ	666	HV	718	JV
563	ES	615	GQ	667	HV	719	JV
564	ES	616	GQ	668	HV	720	JW
565	ES	617	GQ	669	HV	721	JW
566	ET	618	GQ	670	HW	722	JW
567	EU	619	GQ	671	IQ	723	JW
568	EU	620	GR	672	IQ	724	JW
569	EV	621	GR	673	IQ	725	JX
570	EV	622	GR	674	IQ	726	JX
571	EV	623	GR	675	IQ	727	JX
572	EV	624	GR	676	IR	728	JX
573	EV	625	GR	677	IT	729	JX
574	EV	626	GR	678	HW	730	KQ
575	EV	627	GR	679	IT	731	KR
576	EW	628	GR	680	IU	732	KR
577	EW	629	GS	681+	IU	733	BW
578	EW	630	GS	682	IU	734	KR
579	EX	631	GT	683	IV	735	KR
580	EX	632	GT	684	IX	736	KR
581	EX	633	GT	685	IX	737	KS
582	FP	634	GU	686	IX	738	KS
583	FP	635	GU	687	IX	739	KS
584	FP	636	GU	688	JQ	740	KS
585	FQ	637	GV	689	JQ	741	KS
586	FQ	638	GV	690	JQ	742	KS
587	FQ	639	GW	691	JS	743	KS
588	FQ	640	HQ	692	JS	744	KT
589	FQ	641	HQ	693	JS	745	KS
590	FR	642	HQ	694	JS	746	KS
591	FR	643	HQ	695	JS	747	KS

(*Continued*)

TABLE 1. Characteristics and map coordinates of 1004 lakes in the Experimental Lakes Area (ELA), northwestern Ontario. Abbreviations: A_o, surface area (hectares); z_m, maximum depth (meters); SDV, Secchi disc visibility (meters); TDS, total dissolved solids (milligrams/liter); C, conductivity (micromhos/centimeter at 25 C); *, indicates lakes that are not shown on the ELA map; +, indicates lakes that are controlled by the Freshwater Institute, Fisheries Research Board of Canada; shallow, indicates less than 1 m in depth.

Lake	Location	Lake	Location	Lake	Location	Lake	Location
748	KT	800	LU	852	MU	904	OV
749	KT	801	LU	853	MU	905	OV
750	KT	802	LU	854	MU	906	OV
751	KT	803	LU	855	MU	907	OV
752	KT	804	LU	856	MU	908	OV
753	KT	805	LU	857	MU	909	OW
754	KT	806	LU	858	MU	910	OW
755	KU	807	LU	859	MV	911	OW
756	KU	808	LU	860	MU	912	OW
757	KU	809	LU	861	MU	913	OW
758	KV	810	LV	862	MU	914	OX
759	KV	811	LV	863	MU	915	OX
760	KV	812	LV	864	MU	916	OX
761	KV	813	LV	865	MU	917	OX
762	KV	814	LV	866	MV	918	OX
763	KV	815	LV	867	MV	919	OX
764	KV	816	LV	868	LX	920	AV
765	KV	817	LV	869	MV	921	AV
766	KV	818	LV	870	MV	922	AW
767	KV	819	LV	871	MW	923	DS
768	KW	820	KV	872	MW	924	DV
769	KW	821	LV	873	MX	925	DW
770	KW	822	LV	874	MX	926	EU
771	KW	823	LV	875	MX	927	EX
772	KW	824	LV	876	MX	928+	IS
773	KW	825	LW	877	MX	929	KV
774	KX	826	LW	878	MX	930	KW
775	KW	827	LW	879	NS	931	MU
776	KW	828	LW	880	NT	932	LU
777	KX	829	LX	881	NT	933	JT
778	KX	830	LX	882	NT	934+	JT
779	KX	831	MP	883	NU	935	BU
780	KX	832	MQ	884	NU	936	HX
781	KX	833	MQ	885	NU	937	FX
782	KX	834	MQ	886	NV	938	ET
783	LR	835	MS	887	NV	939	GV
784	LQ	836	MS	888	NV	940	JX
785	LR	837	MS	889	NV	941	NU
786	LR	838	MS	890	NW	942	LV
787	LS	839	MS	891	MW	943	LU
788	LS	840	MS	892	NW	944	LX
789	LS	841	MS	893	NW	945	LX
790	LS	842	MS	894	NW	946	KX
791	LS	843	MT	895	NX	947	KX
792	LT	844	MT	896	NX	948	EX
793	LT	845	MT	897	NX	949	DX
794	LT	846	MT	898	NX	950	BX
795	LT	847	MT	899	NX	951	BX
796	LT	848	MT	900	NX	952	AX
797	LT	849	MU	901	OR	953	AX
798	LT	850	MU	902	OR	954	CU
799	LU	851	MU	903	OU	955	AV

(*Continued*)

TABLE 1. Characteristics and map coordinates of 1004 lakes in the Experimental Lakes Area (ELA), northwestern Ontario. Abbreviations: A_o, surface area (hectares); z_m, maximum depth (meters); SDV, Secchi disc visibility (meters); TDS, total dissolved solids (milligrams/liter); C, conductivity (micromhos/centimeter at 25 C); *, indicates lakes that are not shown on the ELA map; +, indicates lakes that are controlled by the Freshwater Institute, Fisheries Research Board of Canada; shallow, indicates less than 1 m in depth.—(*Concluded*)

Lake	Location	Lake	Location	Lake	Location	Lake	Location
956	AU	969	AU	982	JX	995	OR
957	AU	970	AU	983	JX	996	OX
958	AU	971	AX	984	JX	997	NX
959	DQ	972	CW	985	KX	998	NX
960	FQ	973	DS	986	KX	999	MX
961	FS	974	DS	987	KW	1000	MX
962	GQ	975	FX	988	LU	1001	GW
963	GQ	976	FX	989	MX	1002	FS
964	GP	977	FQ	990	NX	1003	BU
965	HP	978	HR	991	NS	1004	FX
966	IQ	979	HU	992	NU		
967	IQ	980	IU	993	NV		
968	IQ	981	JS	994	OR		

Since the lakes were sampled with a bias towards those with areas of 2–50 ha and maximum depths greater than 2 m, the histograms should not be considered as representative of all lakes shown on the insert map. In surface waters of the lakes sampled, total dissolved solids varied from 3 to 140 mg/liter, with a mean of 36 mg/liter. Conductivity ranged from 11 to 161 μmhos/cm, with a mean of 29 μmhos/cm at 25 C.

Acknowledgments

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JOHNSON, W. E., AND J. R. VALLENTYNE. 1971. Rationale, background, and development of experimental lake studies in northwestern Ontario. J. Fish. Res. Bd. Canada 28: 123–128.

Geography and Bathymetry of Selected Lake Basins, Experimental Lakes Area, Northwestern Ontario[1]

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BRUNSKILL, G. J., AND D. W. SCHINDLER. 1971. Geography and bathymetry of selected lake basins, Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Bd. Canada 28: 139–155.

The Experimental Lakes Area (ELA) is located at 93°30′–94°00′W and 49°30′–49°45′N at an altitude of 360–380 m above mean sea level. This area is underlain by Precambrian acid granites overlain in some areas by thin glacial drift composed largely of sand and gravel of quartz, plagioclase, and K-feldspar. The area was under glacial ice about 14,000 years B.P. (before present). With the melting of this glacial ice, ELA was situated on the eastern margin of glacial Lake Agassiz. As Lake Agassiz levels receded, the present lake basins were formed. The ELA watersheds now drain into the Winnipeg River, which is in the Hudson Bay drainage system.

Mean annual temperatures in the vicinity of ELA are between 0.5 and 2.2 C, and annual precipitation is between 500 and 750 mm. Brunisols were observed over sand deposits in the ELA, but considerable variation in soil types and soil depth were also found. ELA is in a boreal (fire-controlled) subclimax forest of jack pine, black spruce, trembling aspen, and white birch. Aquatic macrophytes were scarce in the littoral zone of ELA lakes. Nearby logging operations and hunting and sport fishing have not influenced the immediate watersheds of ELA lakes.

Morphometric maps and measurements are given for 16 lakes in ELA. These lakes vary from 2.5 to 33 m in maximum depth, and from 1.7 to 56 ha in lake surface area. Using estimates of precipitation, evaporation, evapotranspiration, drainage areas, and lake morphometry, a preliminary calculation of theoretical water renewal time is given for these lakes. These values range from 2.6 to 38 years.

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THE Experimental Lakes Area (ELA) is located 52 km east southeast of Kenora, Ont., at 93°30′–94°00′W, 49°30′–49°45′N at an altitude of 360–380 m above mean sea level. The lakes are on the southwestern part of the Precambrian Shield, about 200 km east of the Shield–Ordovician limestone boundary (Fig. 1). The following is a general description of the area. Detailed maps of topography, geology, vegetation, and climate are not yet available for individual drainage basins.

Geology

ELA watersheds were geologically mapped from airborne magnetometer surveys, interpretation of air photographs, and extrapolation from a nearby ground survey of the area east and northeast of lake 466 (Upper Dryberry Lake) (Davies and Watowich 1958). The map of Davies and Pryslak (1967) indicates that ELA is situated on the south lobe of a massive pink granodiorite batholith of Algoman Age, the most recent and most extensive of Precambrian acid-granitic intrusions of this area. This granodiorite is characterized by aplite and pegmatite dikes of quartz and K-feldspars, and smaller proportions of biotite. The mineralogical composition of a typical hand specimen of lake 466 (Dryberry Lake) pink granodiorite determined by Davies and Watowich (1958) is given in Table 1. These minerals are all sparingly soluble in water. A more detailed discussion of the chemistry and weathering of this bedrock is found in Brunskill et al. (1971). Wilson (1965) reviewed the geology of the Rainy River–Kenora districts, as well as the rest of the Canadian Shield.

Ten to 30 km east, south, and west of ELA there is a more complex outcrop series of older sedimentary (Keewatin–Warclub schists, greywackes, gneisses, iron formations), volcanic (Keewatin–Populus lavas, basalts, tuffs), and intrusive rocks

[1]The third in a series of 14 papers on the work of the Fisheries Research Board of Canada, describing background environmental data on the Experimental Lakes Area, northwestern Ontario. For location of numbered lakes see insert map at the back of this issue of the Journal of the Fisheries Research Board of Canada. A key to lake locations is given by Cleugh and Hauser (1971).

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FIG. 1. General location of the Experimental Lakes Area.

(Laurentian and Pre-Laurentian dikes of altered gabbros and hornblende diorite) (Davies and Watowich 1958). These more soluble rock outcrops were not shown on the Kenora–Fort Frances geological map (Davies and Pryslak 1967) as being in ELA watersheds, but pebbles and boulders of chloritic greenstone and tuff were found in the drainage basins of lakes 122, 239, 230, and 241, and these rocks undoubtedly occur throughout the area.

Deposits of economic importance (Au, Cu, Ni, Fe, U, Mo, talc) occur in sedimentary and volcanic outcrops to the south, east, and west of ELA. Several shaft and trench mines were established in 1936 about 60 km south of lake 239 (Davies and Watowich 1958).

In most areas of ELA, the strongly sheared, jointed, and faulted bedrock controls local drainage systems, and many lakes lie in fault basins (unpublished preliminary maps, Ontario Department of

TABLE 1. Mineralogical composition of Dryberry Lake pink granodiorite (after Davies and Watowich 1958).

	%
Quartz (SiO_2)	26
Microcline ($KAlSi_3O_8$)	31
Oligoclase ($Na_{0.7-0.9}$, $Ca_{0.3-0.1}$)($AlSi_3O_8$)	38
Biotite [$K(Mg,Fe)_3$ ($AlSi_3O_{10}$)$(OH)_2$]	3
Magnetite (Fe_3O_4)	3
Sericite [$KAl_2(AlSi_3O_{10})(OH)_2$]	1
Ilmenite ($FeTiO_3$)	0.5
Leucoxene (TiO_2)	0.5
Zircon ($ZrSiO_2$)	0.5
Kaolinite [$Al_4Si_4O_{10}(OH)_8$]	Trace
Sphene ($CaTiSiO_5$)	"
Apatite [$Ca_{10}(PO_4)_6(OH,F,Cl)_2$]	"

Mines; Davies and Watowich 1958). On this bedrock most lakes would be in water-tight basins, except glacial drift-dammed lakes (for example, lake 468, Roddy Lake). Relief in the immediate ELA does not usually exceed 80 m, and maximum relief is usually associated with fault scarps.

The sequence of glacial events in northwestern Ontario was given by Zoltai (1961, 1965a, b, 1967, and references therein), based on interpretation of air photographs and field observations of glacial striae, moraines, stratigraphy of glacial drift, and lacustrine sediments. Zoltai (1961) proposed a tentative correlation of the four ice movements observed in northwestern Ontario with subages of the Wisconsin glaciation. A summary from Zoltai (1961) follows:

(1) The oldest or Keewatin ice movement (which may not have reached ELA) came from the north northwest. The evidence for this glacial advance was based mainly on glacial striae, since subsequent glacial movements removed most of the deposits left by this ice lobe. Keewatin glacial drift was most likely derived from granites and limestones in northwestern Manitoba.

(2) The degree of oxidation of Keewatin glacial drift indicated a considerable ice-free period after deglaciation.

(3) The second or Patrician ice advance came from northeast of ELA and extended into central Minnesota. Glacial drift left by this movement consisted of granitic sands and stones derived from the northeast.

(4) The ice-free period following deglaciation after the Patrician advance was brief, as little weathering was noted in glacial drift of this ice movement.

(5) The third glacial advance came from the northwest and spread calcareous, stony clays (Keewatin in origin) as far east as Fort Frances. Glacial deposits from this ice advance were not found in ELA.

(6) As this ice mass melted, a large proglacial lake (Lake Agassiz) formed, depositing lake clays (sometimes varved) along the eastern shore of the present Lake of the Woods. With further ice recession, this lake drained from the area and its sediments were subjected to subaerial erosion.

(7) A fourth ice advance reached the area from the northeast, covering most of Lake of the Woods and terminating north of Rainy Lake. Granitic glacial drift was deposited over and reworked with Lake Agassiz sediments east of the present Lake of the Woods.

(8) A period of intermittent retreat of this ice mass followed, depositing a series of northwest–southeast-oriented moraines that were sometimes overridden by short readvances of the ice lobe. One of the last ice readvances, the Valders, left a major end moraine (the Hartman) northeast of Dinorwic, Ont., but this ice lobe did not reach ELA. During this recessional period the ice front terminated in Lake Agassiz, which at that time drained south through Lake Traverse in South Dakota–Minnesota into the Mississippi River drainage system. During a high-water stage of Lake Agassiz, a red, calcareous clay was transported by water from an eastern source (perhaps the Thunder Bay area) and was deposited in beds 8–40 cm in thickness as far south as Rainy Lake.

(9) Further melting of the ice sheet opened eastern outlets of Lake Agassiz, lowering its level below the Upper Campbell strandline (Zoltai 1967). ELA was topographically above Lake Agassiz level at this time, although fluctuations of the ice sheet may have recreated a high stage of Lake Agassiz, briefly submerging ELA. With complete deglaciation and crustal rebound, the present drainage was established through the Winnipeg–English rivers to Lake Winnipeg, Nelson River, and Hudson Bay.

The date of retreat of the last ice lobe from the Lake of the Woods area is not known, but it is inferred that it took place prior to the Valders maximum at 11,800 years ago. Prest (1969) indicates that this area was free of ice about 12,500 years ago, although Bryson and Wendland (1967) estimate a date of 10,500 years B.P. for this event.

Lake Agassiz (average water depth 45–75 m in northwestern Ontario, according to Elson 1967) sediments accumulated in the Lac Seul, Wabigoon, and Lake of the Woods basins, and regions between these basins were areas of shallow water and wave erosion (Zoltai 1965a). Lowdon and Blake (1968) reported a radiocarbon date of 9580 ± 220 years

B.P. for organic material in marl from a gravel beach near Emo, which was interpreted by Johnston (1915) as a Campbell-phase strandline of Lake Agassiz (see also Elson 1967 and Zoltai 1961). A projection of this strandline elevation to ELA indicates water levels at about 393 m (see fig. 18 in Zoltai 1967), which would have submerged much of ELA. During this time ELA was probably a shallow region of Lake Agassiz with many islands. With decreasing water levels, ELA lakes were isolated from the Lake Agassiz water mass.

ELA is located between the Wabigoon and Lake of the Woods basins, and has irregularly distributed deposits of bouldery till, stratified sand-silts, and gravel in low-lying areas (Fig. 2*a*, *b*). Some glacial drift deposits near the ELA field laboratory are about 18 m in thickness. Hilltops are of bare rock, and were eroded by lake action (Zoltai 1965a). Only sediments of lakes deeper than 10 m would be expected to include the Agassiz clays and glacial till sequences described by Zoltai (1961).

Soils

Soils in ELA drainage basins have not been studied; the following comments are based on casual observations during field work in the area.

Hilltops and hill slopes in ELA usually have little or no soil, but lower-lying areas often have brunisols, using the terminology of the proceedings of the National Soil Survey of Canada (1968). The brunisols varied between 10 and 30 cm thickness, and consisted of a mixture of partially decomposed plant remains (LF layer) covering bedrock. In certain instances an indistinct eluviated (Aej) horizon occurs just below the LF layer on top of bedrock.

In areas underlain by sand and boulder till, greater thicknesses of orthic brunisols were observed. The surface mor was composed of detritus from coniferous and deciduous trees, tree roots, partially decomposed organic materials, and fungal hyphae. An example of this mor layer (LF) in an exposure south of lake 468 (Roddy Lake) (Fig. 3*a*) was 10–20 cm thick and exhibited a sharp contact with an underlying light gray Ae horizon about 20–25 cm in thickness. A reddish-brown layer of sand 30–50 cm thick beneath the Ae horizon represents some type of B horizon (probably a Bm) that grades into a C horizon of clean quartz and feldspar sand. Zoltai (1965b) characterized similar soils in the area just north of Dryberry Lake, and commented that litter decomposes very slowly on these types of soils. He found the organic horizon (LF) and the leached horizon (Ae) to be very acid. We measured *p*H of runoff water, and obtained values of 4.0–4.5 in some darkly colored soil waters.

Zoltai (1965b) also noted that the present forest vegetation bears little relation to the soils, as similar soils were found under both coniferous and broad-leaved tree stands. He found degraded black (chernozem) soil overlying clay in some areas, which he interpreted as soil developed under prairie vegetation during a milder or drier climate in the past (Zoltai 1965b, and personal communication).

Climate

Weather records for the period 1931–60 from meteorological stations at Kenora and Emo, Ont., demonstrate modification of weather by local environment (Table 2). The proximity of large lakes and different soil types, elevation, and vegetation in the area produce local differences in climate. Zoltai's (1965b) regions 4S and 5S, which include ELA, were climatically characterized from published records (Monthly Record, Canada Department of Transport 1959, 1967; Chapman and Brown 1966).

Annual mean temperatures at the different stations (Table 2) varied between 0.5 and 2.2 C, with a maximal annual mean temperature of 6.1–8.9 C, and a minimal annual mean temperature of –5.0 to –3.9 C. January mean temperatures ranged from –19.4 to –16.1 C, and July mean temperatures were between 18.3 and 20 C. There were about 103 frost-free days, with 140 days free of severe frost, which indicates the length of the terrestrial growing season (Table 3). Total annual precipitation ranged from 500 to 750 mm at different stations in the vicinity of ELA, with about 65% of the precipitation falling from May through September. On the average, there were 122 days in a year when precipitation exceeded 2.5 mm; about half of these days occurred during the growing season. Average annual snowfall ranged from 1500 to 2250 mm. Chapman and Brown (1966) gave an average annual potential evapotranspiration value of 500–550 mm based on Thornthwaite's method of calculation.

The Hydrological Atlas of Canada (1969) indicated runoff to be between 120 and 250 mm from the Lake of the Woods area. Meteorological and hydrological data will be improved when a new meteorological site in ELA (Teggau Lake Station, located just west of lake 239, installed summer 1969) has yielded several years' data for the immediate area.

Average yearly solar radiation for Winnipeg, the nearest station reporting such information, was 117,895 gcal cm^{-2} $year^{-1}$ (16-year average).

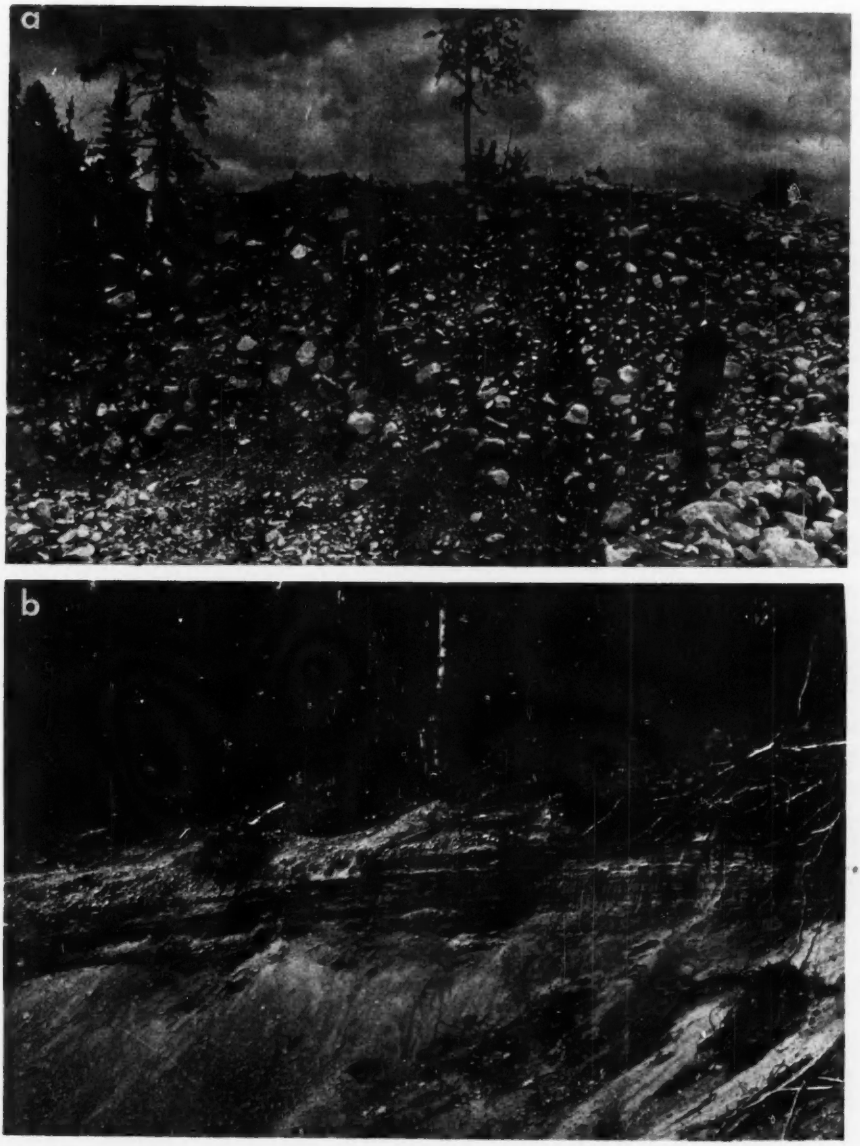

FIG. 2. The local environment of the Experimental Lakes Area: (*a*) boulder till near outlet of lake 114; (*b*) glaciofluviatile sand and silt 3 miles west on road from ELA camp.

FIG. 3. (*a*) Photograph of lake 468 (Roddy Lake) brunisol profile near camp road. Horizons are indicated by symbols. Thickness of horizons is given in the text. (*b*) Understory vegetation, east drainage area of lake 239.

TABLE 2. Average climatic data for two weather stations in northwestern Ontario. Data from Department of Transport climatic summaries (see Zoltai 1965b).

	Kenora					Emo			
	(1940–57) Temp (*C*)		(1940–57) Precipitation		(1923–45)	(1940–41, 1950–57) Temp (*C*)		(1940–41, 1950–57) Precipitation	
Monthly mean	Max / Min	Mean	Total (*cm*)	Snow (*cm*)	Avg wind speed (*mph*)	Max / Min	Mean	Total (*cm*)	Snow (*cm*)
Jan.	−12.5 / −21.5	−17.0	3.51	34.80	9.8	−10.5 / −23.3	−16.9	2.68	26.42
Feb.	−9.4 / −19.5	−14.4	2.95	28.70	10.1	−28.2 / −22.4	−14.9	2.26	21.84
Mar.	−1.9 / −12.4	−7.2	3.45	30.48	10.4	−35.1 / −14.6	−7.5	3.23	28.45
Apr.	+7.6 / −2.9	2.5	3.78	18.02	11.3	9.6 / −3.4	3.1	4.60	12.19
May	16.3 / 4.6	10.5	5.33	3.81	11.0	17.9 / 3.3	10.5	6.20	1.02
June	21.4 / 10.6	16.0	7.80	0.00	10.6	22.6 / 8.7	15.7	9.35	0.00
July	25.1 / 14.1	19.6	8.53	0.00	9.8	26.3 / 12.0	19.1	9.40	0.00
Aug.	23.4 / 13.0	18.1	7.62	0.00	9.5	24.7 / 10.5	17.6	8.66	0.00
Sept.	17.0 / 7.4	12.2	6.45	1.27	10.7	18.9 / 5.4	12.1	7.19	0.25
Oct.	9.6 / 1.7	5.7	3.86	8.64	11.2	12.3 / −0.4	6.0	4.19	3.81
Nov.	−1.9 / −8.0	−5.0	4.70	36.07	10.8	0.4 / −8.6	−4.2	4.75	27.43
Dec.	−9.5 / −18.4	−13.6	3.43	31.75	9.8	−7.3 / −19.1	−13.2	2.90	26.16
Yearly mean	7.1 / −2.5	2.3	Σ=61.41	193.55	$\bar{x}$ = 10.4	$\bar{x}$ = 8.9 / −4.4	2.3	Σ=65.41	147.57

TABLE 3. Average dates of freezing weather at four weather stations in northwestern Ontario. Data from Department of Transport Weather Summaries. Numbers in parentheses are numbers of years for the average.

	0 C and below		
Station	Spring (avg date)	Fall (avg date)	Avg frost-free days
Kenora	May 19	Sept. 24	128(12)
Dryden	June 2	Sept. 11	101(28)
Emo	June 4	Sept. 8	96(28)
Ignace	June 11	Aug. 28	78(34)

The lowest light levels occurred in December (95 gcal cm^{-2} day^{-1}), and the highest in May, June, and July, which averaged 518, 530, and 550 gcal cm^{-2} day^{-1} respectively.

Small (<50 ha) lakes in ELA were usually ice-covered by mid-November, and were ice-free by late April or early May. In these small lakes maximum ice thickness in 1968–70 was about 100 cm, with the ice thickness on most lakes ranging from 50 to 70 cm. About half of this thickness was frozen snow-slush due to water flowing on top of the original ice surface. Snow cover over lake ice varied between 20 and 100 cm in 1967–70. Maximum runoff occurs during and immediately after

ice melt. Larger (>1000 ha) lakes, such as lake 161 (Hillock) and lake 228 (Teggau), were usually ice-covered by late December and were ice-free by mid-May.

Vegetation

Zoltai (1965b) described the regional vegetation in the area between Lake of the Woods–Rainy River and Lac Seul. The tree species were typical of boreal subclimax forests (Rowe 1959) with jack pine, black spruce, trembling aspen, and white birch being dominant. Certain areas with warmer local climates had stands of bur oak and red oak, red and Manitoba maple, basswood, and red and white pine. Zoltai (1965b) listed forest trees in approximate order of decreasing abundance in present stands: jack pine (*Pinus banksiana* Lamb.), black spruce (*Picea mariana* (Mill.) BSP.), trembling aspen (*Populus tremuloides* Michx.), balsam fir (*Abies balsamea* (L.) Mill.), white birch (*Betula papyrifera* Marsh.), white spruce (*Picea glauca* (Moench) Voss), balsam poplar (*Populus balsamifera* L.), black ash (*Fraxinus nigra* Marsh.), red pine (*Pinus resinosa* Ait.), white pine (*Pinus strobus* L.), larch (*Larix laricina* (Du Roi) K. Koch), white cedar (*Thuja occidentalis* L.).

Open-growth jack-pine stands chiefly occupy exposed rock slopes and hilltops in the area. The understory in such stands is principally juniper (*Juniperus communis* L.). Well-drained slopes are occupied by a mixture of jack pine and black spruce. These stands have a well-developed understory of balsam fir, speckled alder (*Alnus rugosa* (Du Roi) Spreng.), hazel nut (*Corylus americana* Walt.), and *Vaccinium* sp.

On thick, well-drained glacial drift, dense stands of black spruce predominate. The canopy in such areas is usually closed, and the understory is limited to mosses, lichens, and *Lycopodium* spp. (Fig. 3*b*) (chiefly *complanatum* L. and *obscurum* L.; also *clavatum* L. and *lucidulum* Michx.).

Trembling aspen and white birch are scattered among all of these communities, except for a few pure stands on exposed areas. Black ash occurs only in small clumps on relatively moist sites. White cedar appears to be limited to the very edge of lakes. It seldom appears more than 2 m above water level.

Boggy areas are covered by a mixture of black spruce, alder, and tamarack (*Larix laricina* (Du Roi) K. Koch.). The shrubs Labrador tea (*Ledum groenlandicum* Oeder.), swamp laurel (*Kalmia polifolia* Wang), leather leaf (*Andromeda glaucophylla* Link.), *Betula glandulosa* Michx., and bog rosemary (*Chamaedaphne calycutata* (L.) Moench) occur on the sphagnum mat along shorelines in such areas.

Red pine is confined to lakeshores or sandy ridgetops where it occurs in nearly pure stands. The stands in such areas are usually more open than jack-pine–spruce stands, allowing some trees to escape fires; therefore these trees often reach ages in excess of 300 years. Red and white pine and the climax species white spruce and balsam fir have had their distribution in ELA greatly reduced by successive fires. Assuming that fires can be dated by the usual procedures of ageing fire scars of jack-pine regrowth, it appears that small, rather localized fires have swept the area repeatedly at intervals of perhaps 25–50 years. The last widespread fire was 100–110 years ago. Parasitism by dwarf mistletoe (*Arceutholium pusillum* Peck) is mainly confined to black spruce in boggy areas, indicating that bogs escaped most fires to form a seed source for upslope stands of black spruce on sites where white spruce would normally dominate.

Other species occasionally found in ELA include white elm (*Ulmus americana* L.), largetooth aspen (*Populus grandidentata* Mich.), and red maple (*Acer rubrum* L.) in the upper story; and mountain maple (*Acer spicatum* Lam.), pin cherry (*Prunus pennsylvanica* L.f.), and chokecherry (*Prunus virginiana* L.) in the understory. Macrophytes are scarce in the littoral zone of lakes. Table 4 gives most common species with notes on habitat. The list is not complete.

As previously mentioned, it is likely that the climate was milder in western Ontario in the past (Bryson et al. 1965; Zoltai 1965b). It is thus probable that past vegetation may have had greater proportions of deciduous hardwoods and grassland species.

Human Population and Land Use

Prior to European immigration, northwestern Ontario was inhabited by the migratory Ojibwa (Chippewa) Indian tribe, generally in bands of less than 300 (Jenness 1967). Since this tribe did not practice agriculture, their activities on the land near Lake of the Woods were probably limited to hunting moose, deer, and fur-bearing animals (beaver, otter, ermine), fishing, and harvesting wild berries and wild rice (Jenness 1967). From the late 17th to mid-19th century, the Rainy River–Lake of the Woods–Winnipeg River waterway was an important canoe route for shipping supplies and furs to and from fur trading posts on Lake Winnipeg and points west. Some early canoe routes in the vicinity of ELA are given in Davies and Watowich (1958). A brief history of development

TABLE 4. Aquatic macrophytes found in ELA, summer 1970.

Species	Lake examples	Notes
Isoetes sp.	305,240	Sandy or silty areas. To depth of 3–4 m.
Equisetum fluviatile L.	305,470,468	Most common emergent species.
Typha latifolia L.	239	Small patches.
Sparganium angustifolium Michx.	470	Common on marshy shores and *Sphagnum* mats.
Sparganium multipedunculatum (Morong.) Rydb.	470	Common on marshy shores and *Sphagnum* mats.
Potamogeton amplifolius Tuckerm.	239,305	
Sagittaria latifolia Willd.	239,305,468,317	Common.
Scirpus spp.		Small patches.
Carex spp.	Most lakes	Widespread.
Calla palustris L.	632,314	Common on marshy shores and *Sphagnum* mats.
Eriocaulon septangulare With.	239,240,305	Widespread in sand or silt–clay sediment to a depth of 3–4 m.
Iris versicolor L.		Very common.
Nymphaea odorata Ait.	320	Rare in most ELA lakes.
Nuphar microphyllum (Pers.) Fernald.	305,470	Widespread; abundant in shallow pools.
Nuphar variegatum Engelm.	261,305,468	Widespread.
Drosera rotundifolia L.	470,118	Common on marshy shores and *Sphagnum* mats.
Drosera intermedia Hayne	470,118	"
Sarracenia purpurea L.	118,470,314,304	"
Lobelia dortmanna L.	240	Sandy or silty areas.
Utricularia purpurea Walt.	470	Silty shores.
Utricularia cornuta Michx.	470	Silty shores.
Utricularia vulgaris L.	240,239,470	Shallow silty water.

and hydrological measurements in the late 1800's and early 1900's is given in White and Meyer (1915).

At present, a railroad and the Trans-Canada Highway pass 25 km north of ELA (Fig. 1). Kenora (population 11,060), Sioux Narrows (353), and Dryden (6448) are within 75 km of ELA and are largely supported by the pulp and paper industry, tourism, and sport fishing and hunting. The immediate drainage areas of the lakes under study have not been influenced by these activities.

The Ontario–Minnesota Pulp and Paper Company, Ltd., is involved in logging activities based at a camp (L. 314, winter population 125) at the north end of lake 161 (Hillock). Logging operations were begun in 1953, and are centered at present in the areas north, south, and west of lake 467 (MacDonald). Provincial government regeneration programs for cutover areas involve scarification (rough cultivation) and reseeding of jack pine and black and white spruce.

The Dryden Pulp and Paper Company, Ltd., in operation since 1908, is involved in similar logging activities near Eagle Lake, Wabigoon Lake, and Lac Seul, to the north and east of ELA. There has been no logging in the drainage basins of the lakes under study.

Bathymetric Data for Experimental Lakes

ELA lakes were selected according to the following criteria: (*a*) accessibility; (*b*) volume of lake suitable for experimental manipulation; and (*c*) morphometry suitable for development of thermal stratification (see Johnson and Vallentyne 1971). Bathymetric charts of several lakes were prepared from sonar transects between shore stations located from air photographs. A Raytheon Model DE 119D (200 Kc transducer) Fathometer and an Apelco Depth Sounder (75 Kc transducer) were calibrated by detecting a Secchi disc at known depths. Outlines of lake shores were prepared by projecting transparencies made from aerial photographs taken from 2750 m altitude. Horizontal control was achieved by measuring distances between shore stations located from aerial photographs. Some error probably resulted from these techniques, especially when flight lines for aerial photographs were not directly over the lake being mapped. In many instances, replicate sonar transects were made, and several horizontal control measurements were obtained.

The bathymetric data for lakes under study are given in Table 5 and Fig. 4–17. A comparative

TABLE 5. Morphometric parameters for selected lakes in ELA. Notation and definitions follow Hutchinson (1957).

Lake	A_d, land drainage area ($10^4 m^2$)	A_o, lake surface area ($10^4 m^2$)	V, lake volume ($10^5 m^3$)	$\bar{z}$, mean depth (m)	z_m, maximum depth (m)	L, length of shoreline (m)	D_L, development of shoreline[a]	D_V, development of volume[b]
114	45	12.1	2.07	1.7	5.0	2180	1.17	1.04
120[c]	60	9.31	7.04	7.6	19.0	2130	1.97	1.19
122	76[d]	12.2	8.80	7.2	12.8	1660	1.34	1.70
132	27	7.17	2.37	3.3	8.4	1860	1.96	1.18
227	49	5.00	2.21	4.4	10.0	909	1.15	1.33
230	4.4	1.67	1.04	6.2	13.6	523	1.14	1.37
239	260	56.1	59.1	10.5	30.4	4480	1.69	1.04
240	570[e]	44.1	26.7	6.1	13.1	3440	1.46	1.39
241	32	1.75	0.965	5.5	12.5	565	1.21	1.33
261	37	5.57	1.60	2.9	9.6	1280	1.53	0.90
265	55	13.1	12.8	9.8	18.6	1680	1.31	1.58
302	78	23.7	12.9	5.4	13.8	4280	1.37	1.18
302N	–	12.8	7.32	5.7	13.8	2150	1.70	1.24
302S	–	10.9	5.54	5.1	10.6	2130	1.82	1.44
303	53	9.93	1.50	1.5	2.5	1730	1.54	1.78
304	33	3.62	1.15	3.2	6.7	827	1.23	1.42
305	180[f]	52.0	78.6	15.1	32.7	4900	1.92	1.38
161 (Hillock)	~1360	~1008						
464 (Highwind)		~770						
465 (Mad Dog)		~181						
228 (Teggau)	~1275	~1322						

[a] $D_L = \frac{L}{2\sqrt{\pi A_o}}$.

[b] $D_V = \frac{3\bar{z}}{z_m}$.

[c] Detailed morphometric data for lake 120 will be published at a later date.

[d] Includes land drainage area of lake 123.

[e] Includes land drainage of lakes 239, 303, 304, and shallow ponds 470, 661 between lakes 304–303 and lake 240.

[f] Includes land drainage area of lake 227.

analysis similar to that of Gorham (1958) revealed that lake surface area increases with increasing drainage area and maximum depth, and that mean depth increases with increasing maximum depth. Nearly all of the smaller lakes are sheltered from direct wind stress by hills and trees at the shore line. Lakes 261, 227, 230, and 241 are perched basins about 30–40 m above nearby lakes. These perched basins obviously do not have significant subsurface (groundwater) outflow. Many of the lake basins in ELA probably resulted from glacial ice excavation and deepening of faulted and jointed bedrock topography (Hutchinson 1957, type 26). Some of the larger lakes may be dammed by glacial drift.

Lakes 114, 120, 132, 304, 303, 239, and 240 drain south into lake 466 (Dryberry) and from there into Lake of the Woods. Lake 122 has no surface outlet, but probably has a subterranean outlet into lake 161 (Hillock), which drains to lake 466 (Dryberry). The other lakes under study (227, 302, 305, 261, 265, 230, 241) drain north into Eagle Lake and the Wabigoon–English rivers. Outflows from Lake of the Woods and the English River meet in the Winnipeg River north of Minaki, Ont.

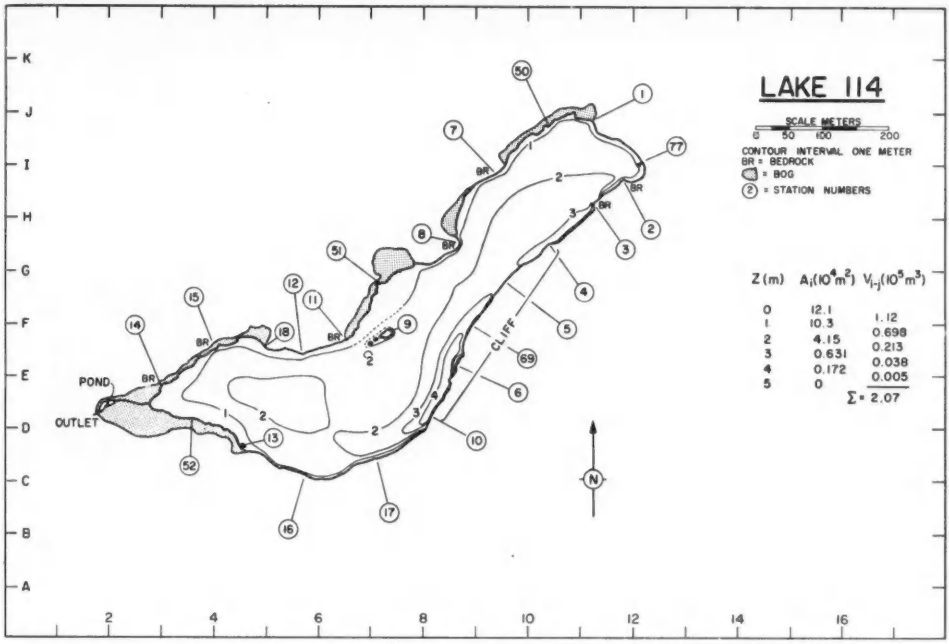

FIG. 4. Bathymetric chart of lake 114.

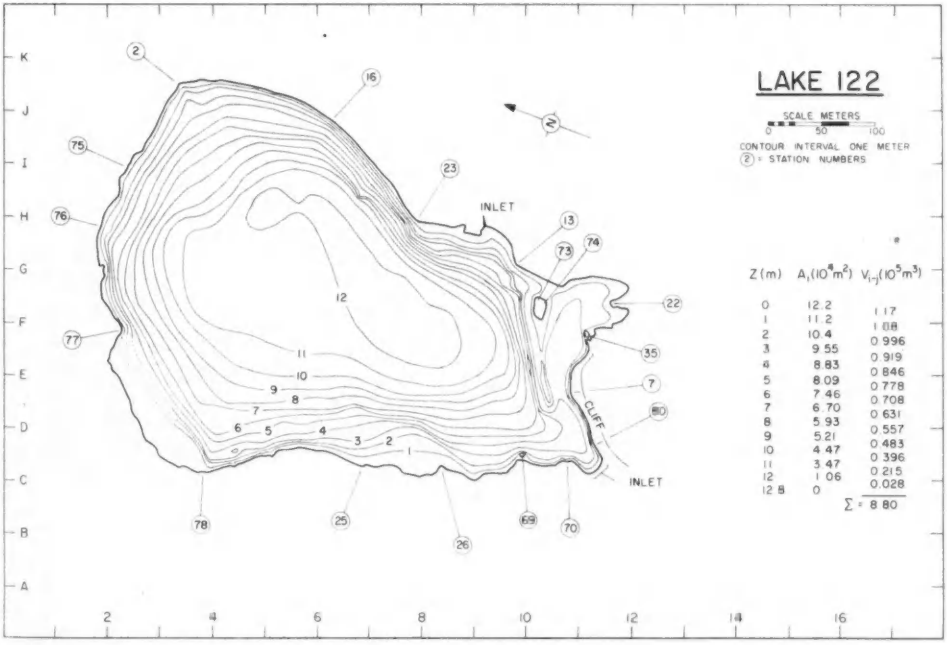

FIG. 5. Bathymetric chart of lake 122.

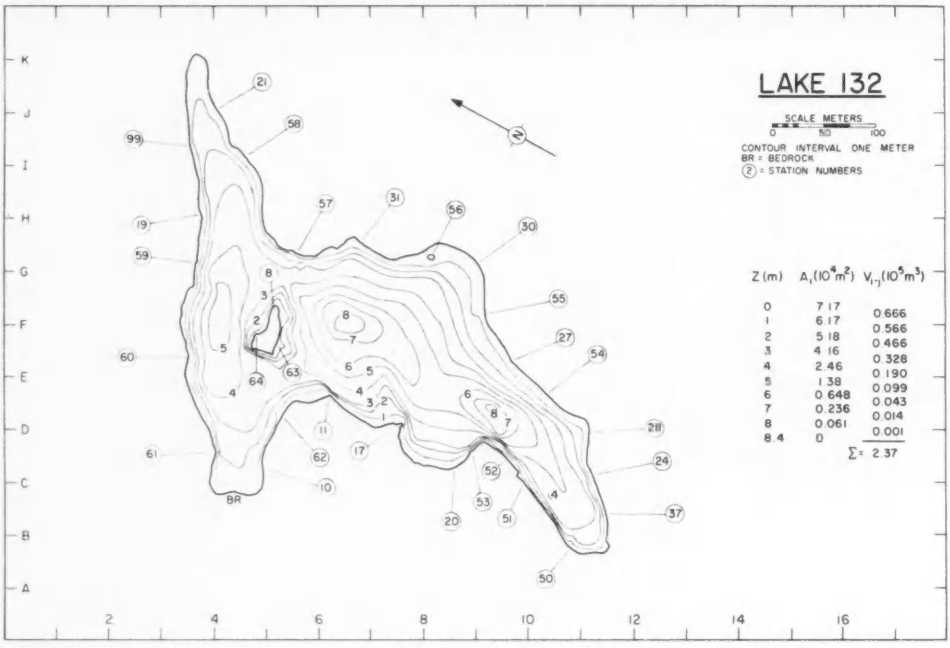

FIG. 6. Bathymetric chart of lake 132.

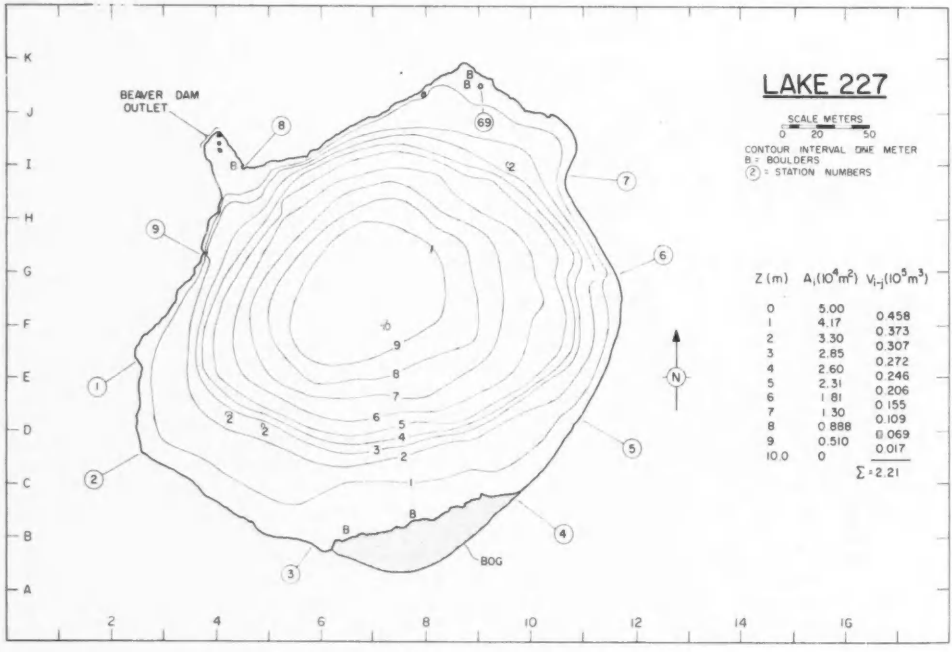

FIG. 7. Bathymetric chart of lake 227.

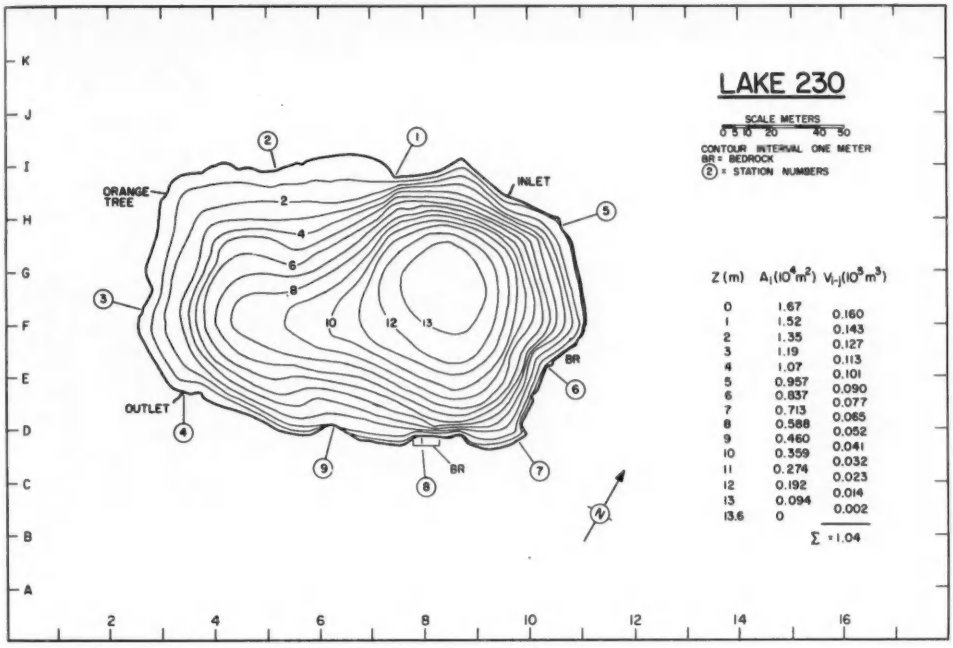

FIG. 8. Bathymetric chart of lake 230.

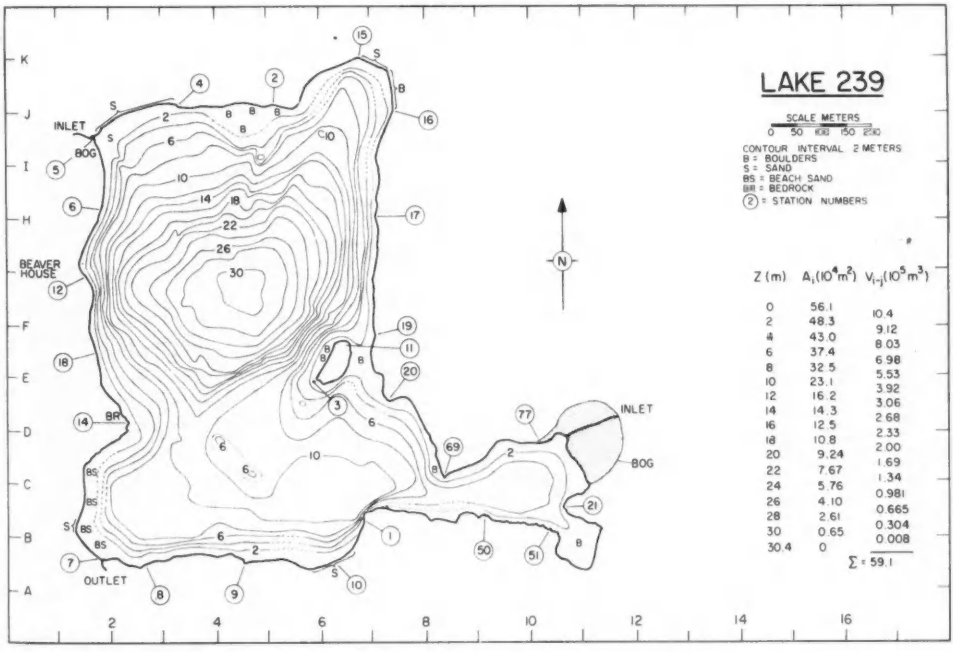

FIG. 9. Bathymetric chart of lake 239.

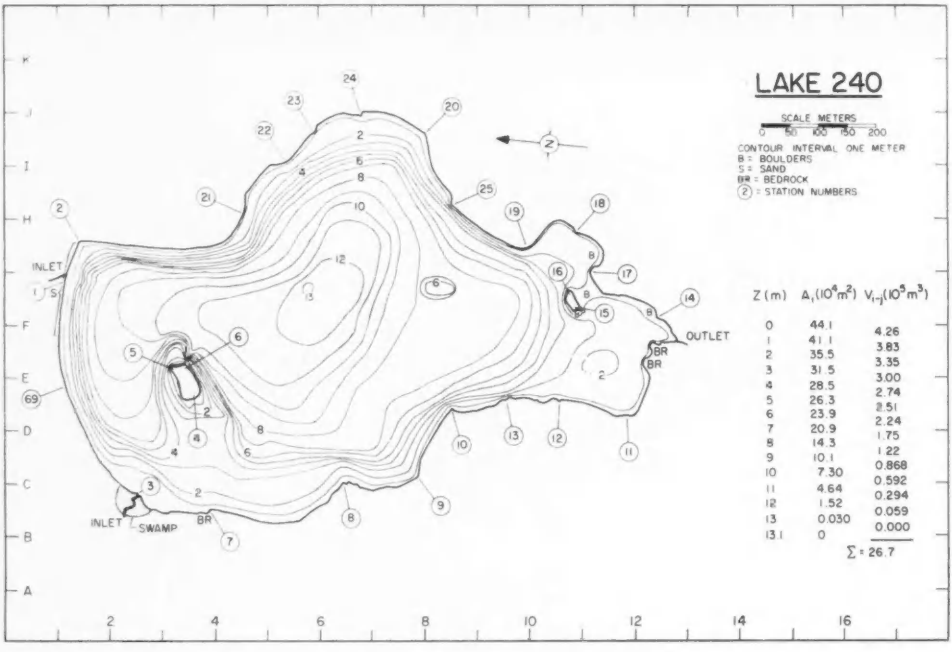

FIG. 10. Bathymetric chart of lake 240.

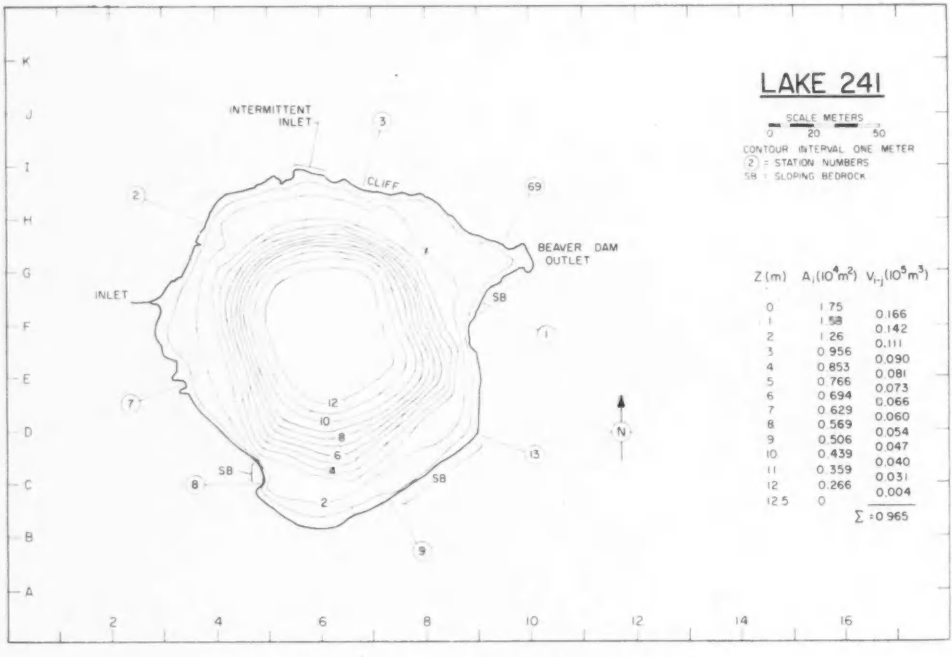

FIG. 11. Bathymetric chart of lake 241.

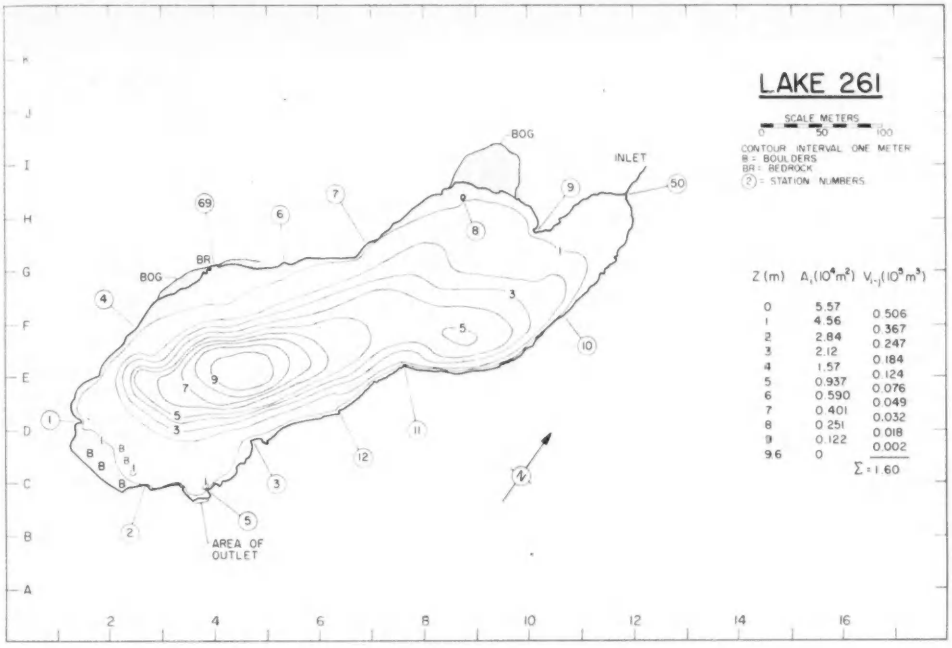

FIG. 12. Bathymetric chart of lake 261.

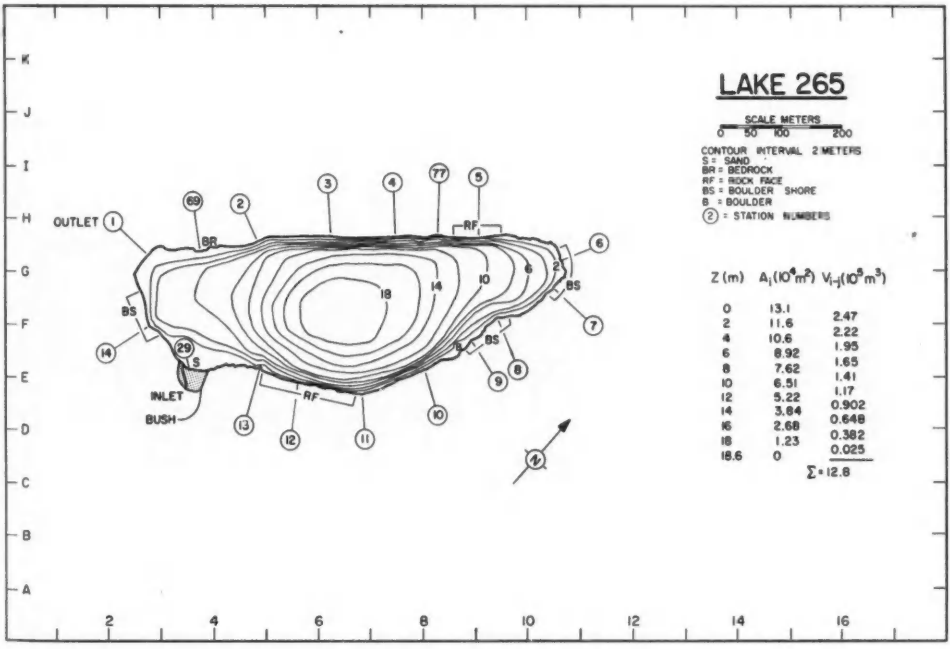

FIG. 13. Bathymetric chart of lake 265.

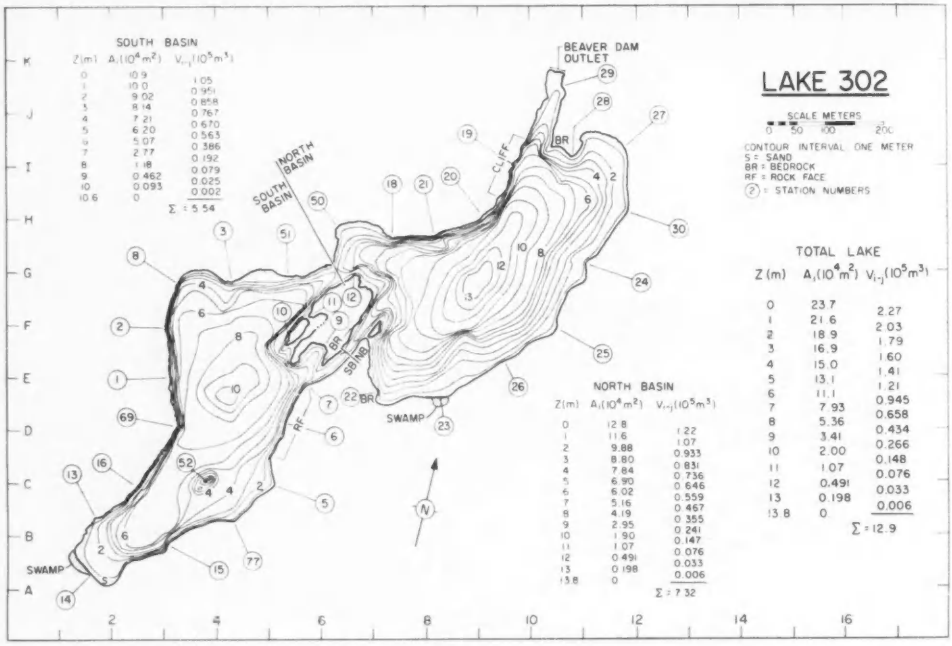

FIG. 14. Bathymetric chart of lake 302.

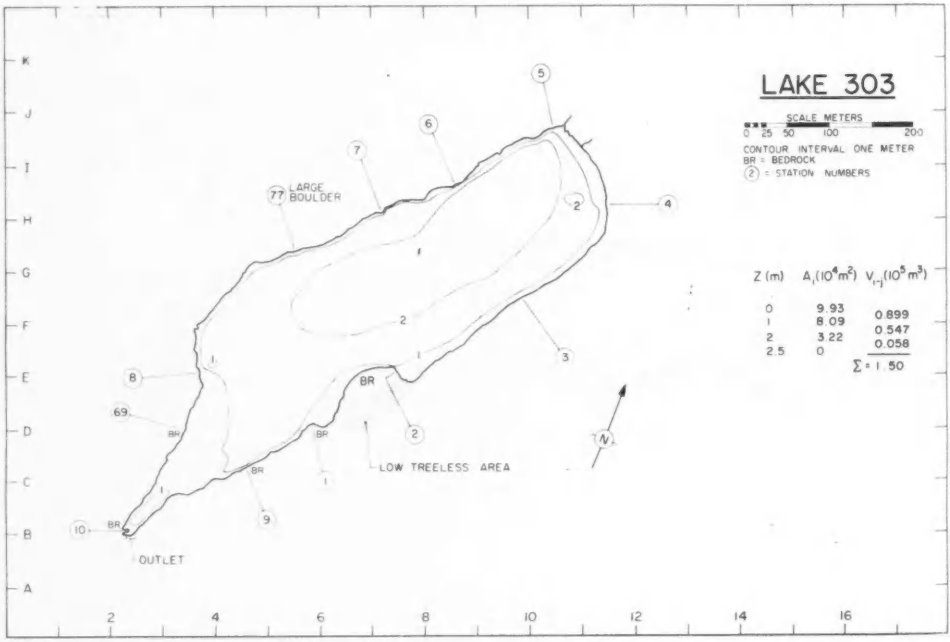

FIG. 15. Bathymetric chart of lake 303.

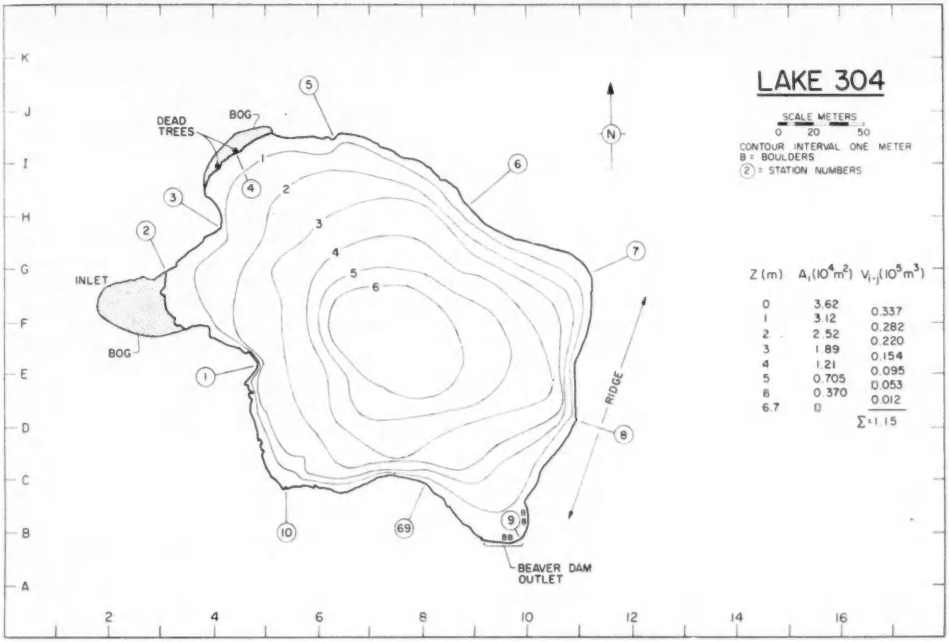

FIG. 16. Bathymetric chart of lake 304.

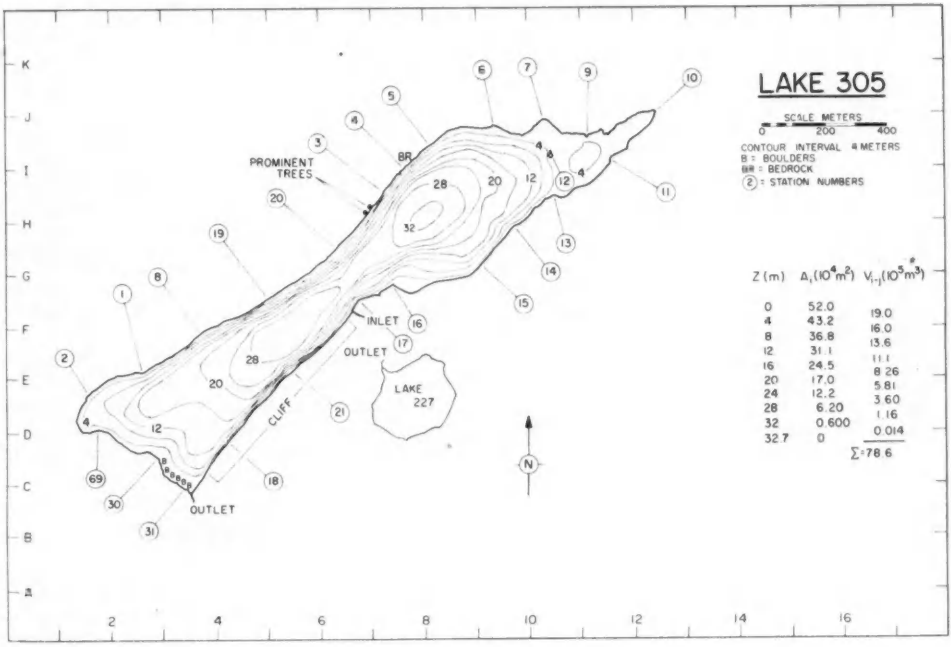

FIG. 17. Bathymetric chart of lake 305.

TABLE 6. Data for the computation of theoretical water renewal time (τ) in selected lakes from ELA. Symbols are explained in the text.

Lake	A_d ($10^4 m^2$)	A_o ($10^4 m^2$)	$(P-E)A_o$ ($10^3 m^3$)	$(P-E_l)A_d$ ($10^3 m^3$)	V_o ($10^3 m^3$)	τ (years)
114	45	12.1	4.11	46.8	50.9	4.1
120	60	9.31	3.17	62.4	65.6	11
122	76	12.2	4.15	79.0	83.2	11
132	27	7.17	2.44	28.1	30.5	7.8
227	49	5.00	1.70	51.0	52.7	4.2
230	4.4	1.67	0.568	4.58	5.15	20
239	260	56.1	19.1	270.4	290	20
240	570	44.1	14.99	592.8	608	4.4
241	32	1.75	0.595	33.3	33.9	2.8
261	37	5.57	1.89	38.5	40.4	4.0
265	55	13.1	4.45	57.2	61.7	21
302	78	23.7	8.06	81.1	89.2	14
303	53	9.93	3.38	55.1	58.5	2.6
304	33	3.62	1.23	34.3	35.5	3.2
305	180	52.0	17.7	187.2	205	38

Some Preliminary Hydrological Calculations

Water and chemical elements are supplied naturally to a lake by direct precipitation on the lake surface, by surface and stream runoff, and by groundwater flow. A detailed study of evaporation, evapotranspiration, outflow from lakes, and the above-mentioned parameters has begun, with participation from several government agencies and university scientists. It will be several years before reliable long-term averages are obtained. We give here a series of preliminary calculations that will allow order-of-magnitude hydrological comparisons among lakes in ELA.

Theoretically, water reaching a lake in a year is the sum of (precipitation – evapotranspiration) on the terrestrial drainage basin and (precipitation – evaporation) at the lake surface. This sum, divided by lake volume, is an estimate of the theoretical annual water renewal coefficient (π, the fraction of lake volume lost to outflow in a year). The reciprocal of this coefficient, often called retention, residence, or turnover time, is termed by us theoretical water renewal time (τ, the number of years necessary to completely replace the lake volume). A mixed water mass is assumed. Theoretical water renewal time (τ) for each lake will be more directly calculated by dividing lake volume by annual outflow when such data become available. The lake basins under consideration are assumed not to have significant groundwater flow out of the basin.

Precipitation data are available from several meteorological stations near the ELA (summarized in Table 2 and Zoltai 1965b). Average annual evapotranspiration for the area has been calculated by Chapman and Brown (1966). Using an average precipitation of 615 mm (Kenora, Ont.), a lake evaporation estimate of 580 mm (Bruce and Weisman 1967) and an evapotranspiration estimate of 510 mm (based on the equation of Penman as cited in Bruce and Weisman 1967), a preliminary calculation of τ is given in Table 6. These hydrological estimates are likely to be useful only for comparison of relative differences in τ for different lake basins within ELA.

Table 6 gives land drainage area (A_d), lake surface area (A_o), A_o multiplied by average annual precipitation minus average annual evaporation ($A_o[P-E]$), A_d multiplied by average annual precipitation minus average annual evapotranspiration ($A_d[P-E_l]$), average volume of water leaving the lake annually ($V_o = A_o[P-E] + A_d[P-E_l]$), and theoretical water renewal time ($\tau = \frac{V}{V_o}$, where V = lake volume). Land drainage area, lake surface area, and lake volume are taken from Table 5. The range of values for τ is large (2–38 years). These ranges of variation in morphometry and τ are critical parameters in present and future experimental lake manipulations.

Acknowledgments

Mr J. H. Russell did most of the field work and preliminary drafting of the bathymetric charts. He was assisted by P. Campbell, D. Mayhood, B. Novén, J. Gray, and R. Bell. S. C. Zoltai and M. J. Capel provid-

ed useful comment and criticism of the manuscript. Mr G. Garner of Ontario–Minnesota Pulp and Paper Co., Ltd., and Mr R. Bunney of Dryden Pulp and Paper Co., Ltd., provided information and historical data for the area. Dr J. E. Nighswander identified many of the terrestrial and aquatic plants and furnished valuable notes on botanical communities of the area.

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Light, Temperature, and Oxygen Regimes of Selected Lakes in the Experimental Lakes Area, Northwestern Ontario[1]

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SCHINDLER, D. W. 1971. Light, temperature, and oxygen regimes of selected lakes in the Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Bd. Canada 28: 157–169.

Light was measured in several Experimental Lakes Area (ELA) lakes in 1968 and 1969, using a Secchi disc, a standard photometer (cadmium sulfide cell), and a 16-channel spectroradiometer. The results of some checks upon the standard procedure usually used for making subsurface light measurements are presented. Light penetration at several wavelengths and total energy flux at several depths are given for a number of lakes. Oxygen and temperature isopleths, winter rates of oxygen depletion, annual heat budgets, and data on work of the wind are also presented. Vertical extinction coefficients (average of all visible wavelengths) ranged from 0.285 for lake 161 to 1.732 for lake 227, and Secchi disc visibility from 1.2 to 10.1 m. The wavelength of maximum transmittance shifted toward long wavelengths, as expected, when transmission coefficients and Secchi disc visibility decreased.

Annual heat budgets ranged from 8400 to 24,200 cal/cm². From 3700 to 16,000 cal/cm² of this were summer heat income. Summer and annual heat budgets were larger for larger lakes. Annual and summer heat incomes were related to mean depth, surface area, and volume of the lakes by simple linear regression equations.

The work of the wind and its efficiency in distributing summer heat income are discussed. The depth of the thermocline in ELA lakes was set early in the year, and did not change during the summer until well after the lake had reached maximum heat content. The temperature of the epilimnion followed the mean daily air temperature closely during the summer though remaining several degrees higher, probably as the result of radiant heating. It is concluded that wind work calculated by Birge's method (Trans. Wis. Acad. Sci. Arts Lett. 18: 341–391, 1916) is of little value, unless corrections for back-radiation and evaporation can be made.

Rates of oxygen depletion under ice were compared in several lakes. Values ranged from 15.0 to 73.8 mg $O_2/m^3 \cdot$day and from 36 to 253 mg $O_2/m^2 \cdot$day.

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LIGHT, temperature, and oxygen data are necessary for the interpretation of physical, chemical, and biological phenomena in lakes. The purpose of this paper is to present such data for selected lakes in the Experimental Lakes Area (ELA) for comparison with other well-studied lakes, and as baseline information for future experimental manipulation of the ELA lakes.

Standard procedures for calculating heat budgets, light extinction, and oxygen deficits have been described elsewhere (Hutchinson 1957; Vollenweider 1961, 1969). No detailed explanation of methods is therefore given here, except where the procedures deviate from standard ones.[a] The effects of the light, temperature, and oxygen regimes upon other components of lake ecosystems are described in other papers of this series (see particularly Armstrong and Schindler 1971; Schindler and Holmgren 1971; Stockner and Armstrong 1971; Patalas 1971; Hamilton 1971).

[1]The fourth in a series of 14 papers on the work of the Fisheries Research Board of Canada, describing background environmental data on the Experimental Lakes Area, northwestern Ontario. For location of numbered lakes see insert map at the back of this issue of the Journal of the Fisheries Research Board of Canada. A key to lake locations is given by Cleugh and Hauser (1971).

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Light

MATERIALS AND METHODS

Total solar radiation was recorded by means of an Eppley pyrheliometer on a tower above 10 m of water near the middle of lake 239 (coordinates D.5–5.0 in fig. 9 of Brunskill and Schindler 1971). In addition, a 16-channel submersible spectroradiometer (photomultiplier type cell) (Agricultural Specialties Co. Ltd.,

Beltsville, Maryland) was used for subsurface light measurements. Routine light measurements were also made with a 25-cm diam Secchi disc and with a Whitney model LMT-8A submersible photometer (cadmium sulfide cell).

All measurements were made between 10:00 AM and 2:00 PM. Spectroradiometer measurements were made only on cloudless or uniformly overcast days.

Results

Turbidity does not have an important effect upon lake transparency in ELA lakes (Fig. 1). Dissolved and colloidal coloring matter appear to determine the depth of the euphotic zone to a very large degree. Birge and Juday (1934) found that most of the light attenuation in humic Wisconsin lakes on Precambrian Shield was due to dissolved coloring matter.

Photosynthetically useful light reaching any depth may be calculated by plotting langleys/mμ against filter wavelength for the spectroradiometer at that depth, then integrating the area bounded by the curve between 400 and 700 mμ (Fig. 2*a–h*). All measurements shown were made in midsummer and near midday of cloudless days, at depths where phytoplankton production was measured (Schindler and Holmgren 1971). The surface light profile was actually taken with the photohead held about 2 cm below the lake surface. The percent of surface light from 400 to 700 mμ reaching a depth did not vary by more than a few percent at different times of the day, as shown by a series of measurements made throughout the day on lake 239.

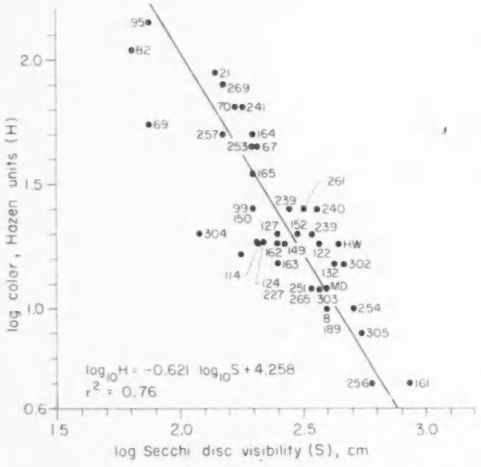

FIG. 1. Relation between Secchi disc visibility and water color for ELA lakes.

A common limnological calculation is the average vertical extinction coefficient of light in water, $\bar{\epsilon}_p^{\lambda}$. Vollenweider (1961) gave the formula:

$$\bar{\epsilon}_p^{\lambda} = -\ln \bar{T} \quad (1)$$

where

$$\bar{T} = 1/3\ (T_{430} + T_{530} + T_{630}), \quad (2)$$

i.e., the transmission per meter at 430, 530, and 630 mμ, respectively. Many other authors have recommended the use of a single filter, with a maximum absorbance at about 530 mμ. The validity of such techniques may be quite easily tested with the spectroradiometer by comparing the $\bar{\epsilon}_p^{\lambda}$ calculated from all wavelengths (Table 1). It is apparent that the above three filters give very good estimates of average extinction for visible light. Single filters do not give good average values, probably because of the great differences in transmission properties of different lake waters for different wavelengths.

Also of some interest is $\epsilon_p^{\lambda\ max}$, the vertical extinction coefficient for the wavelength penetrating deepest in the water, since some authors prefer this to $\bar{\epsilon}_p^{\lambda}$ in modelling photosynthesis–depth relations (see Vollenweider 1960 for a discussion). Table 1 indicates that $\epsilon_p^{\lambda\ max}$ cannot be accurately calculated for all types of lakes unless a wide variety of filters is available. $\bar{\epsilon}_p^{\lambda}$ is undoubtedly the more accurate measurement to be obtained from simple field photometers. It should also be noted that while agreement between equation 2 and extinction of total visible energy is very good, inclusion of ultraviolet and infrared wavelengths generally lowers the calculated average transmission of light, as would be expected, since these wavelengths are more effectively absorbed by water. $\bar{\epsilon}_p^{\lambda}$ as calculated by Vollenweider's recommended formula and filters must therefore be considered to represent extinction of visible light only.

Secchi disc visibility was also compared with light transmission ($\bar{T}$) (Table 1 and Fig. 3). The equation relating Secchi disc visibility (S) to visible light transmittance ($\bar{T}$) is:

$$\bar{T} = 0.055\ S + 0.172 \quad (3)$$

with $r^2 = 0.92$. It is unlikely that this relation can be applied outside ELA (see Vollenweider 1969 p. 171).

Agreement between measurements of the percentage of surface light at various depths determined with the simple Whitney photometer as described above, and total energy of visible light measured simultaneously with the spectroradiometer was very good in most instances (Fig. 4).

Hillock Lake waters displayed light transmission properties very similar to those of distilled water

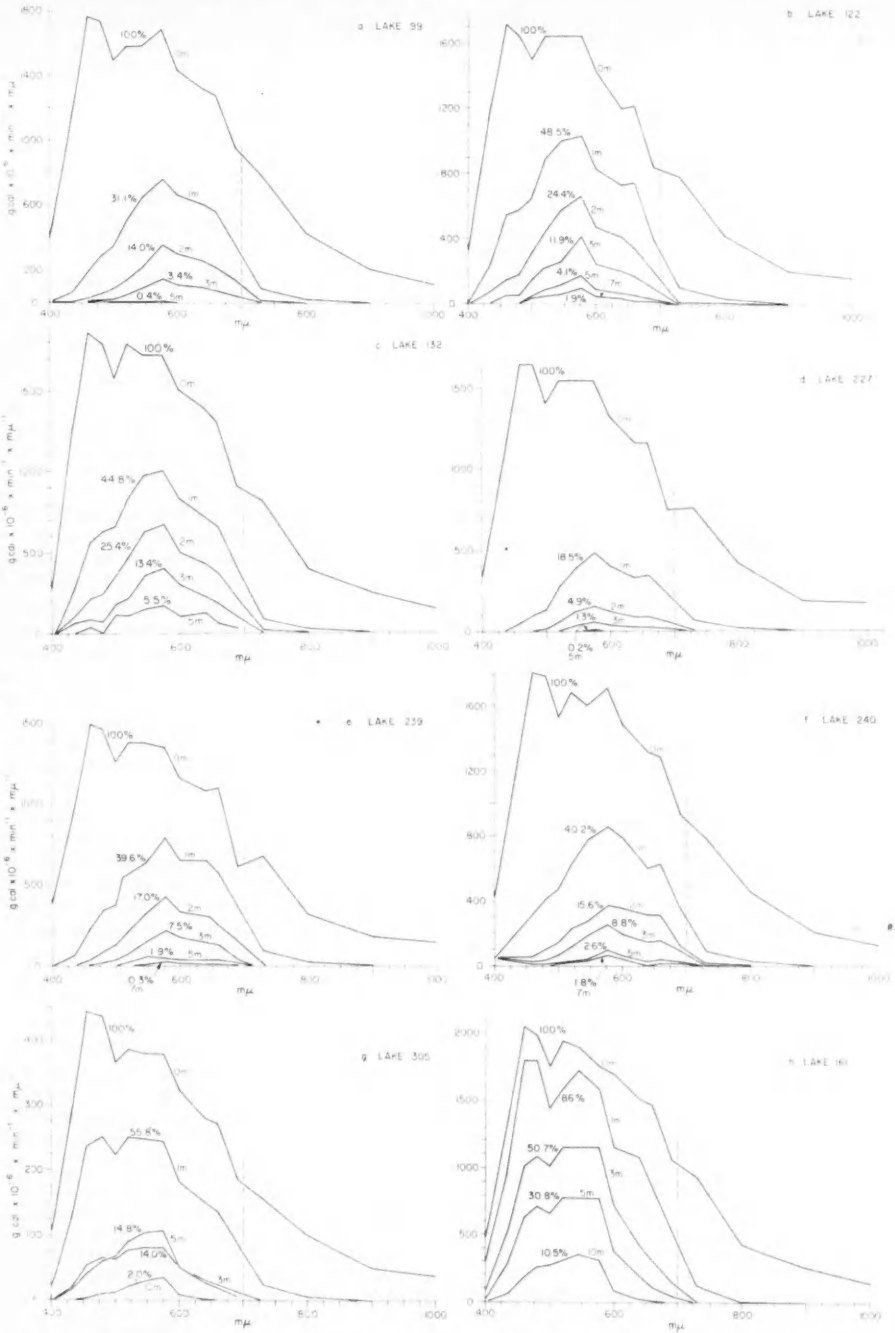

FIG. 2. Percent of incident solar radiation of various wavelengths reaching depths where primary production was measured for several lakes. Percentages are shown of solar energy at photosynthetically active wavelengths (=400–700 mμ) reaching each depth. The crossing of the 3- and 5-m curves on Fig. 2*g* (lake 305) is inexplicable, appearing on two separate occasions.

TABLE 1. Comparison of vertical extinction coefficients, ϵ_v^λ and $\epsilon_v^{\lambda\ max}$, calculated in different ways. All measurements were made with the 16-channel spectroradiometer. Symbols are defined in the text.

	Lake							
	161 (Hillock)	305	239	240	227	122	132	99
ϵ_v^λ avg of all wavelengths	0.537	0.875	1.238	1.287	1.952	1.053	1.133	1.470
ϵ_v^λ avg of 430, 530, 630 mμ	0.277	0.622	0.970	1.047	1.814	0.799	0.894	1.248
ϵ_v^λ avg for 400–700 mμ	0.285	0.620	0.994	1.047	1.732	0.812	0.892	1.228
$\epsilon_v^{\lambda\ max}$	0.095	0.429	0.511	0.637	1.115	0.468	0.540	0.777
mμ of $\epsilon_v^{\lambda\ max}$	480 & 546	546	640	600	577	577	577	600
Color of millipore filtered water	Blue	Green	Yellow-orange	Yellow-orange	Yellow	Yellow	Yellow	Yellow-orange
Secchi depth, *m*	10.1	7.5	4.0	3.75	1.2	4.3	3.7	2.7
T, transmission/m, 400–700 mμ	0.752	0.538	0.370	0.351	0.177	0.444	0.410	0.293

(Fig. 5), except for the second transmission maximum at green wavelengths. Lake 305, which is also very oligotrophic (clear and unproductive), has maximum transmission at green wavelengths. The majority of lakes, however, transmit most strongly in the yellow or orange.

Temperature

MATERIALS AND METHODS

In 1968 temperatures were measured with a Yellow Springs model 43-TR thermistor, accurate to about 1 C. In 1969 a Whitney model TC-5A was used, capable of measuring temperature to about 0.1 C. Thermistors were checked against a mercury thermometer calibrated by the U.S. National Bureau of Standards.

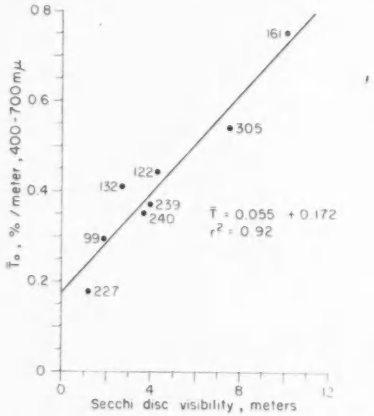

FIG. 3. Relation between light transmission per meter and Secchi disc visibility for several lakes in the area.

RESULTS

Examples of the first, second, and third order lakes described by Whipple (1898; see also Hutchinson 1957) are all found in ELA.[2] Small lakes

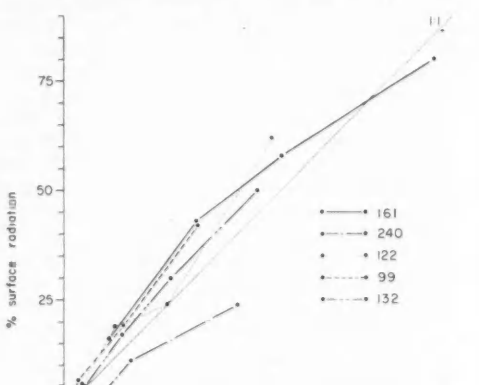

FIG. 4. Relation between measurements of light penetration made simultaneously with a calibrated spectroradiometer (reading directly in units of energy) (abscissa) and a standard Whitney submersible photometer (cadmium sulfide cell) (ordinate).

[2]First and second order lakes have thermal stratification, the former with bottom temperatures near 4 C and the latter with bottom temperatures sufficiently above 4 C to limit heat entering the lake. Third order lakes are not thermally stratified (Hutchinson 1957 p. 439–440).

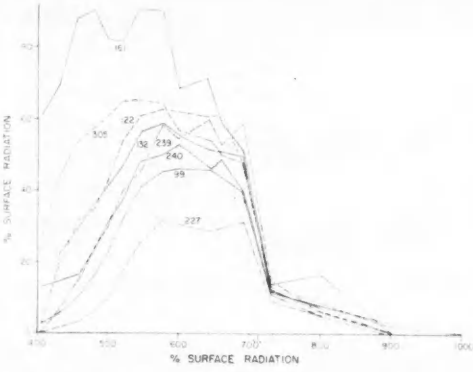

FIG. 5. Percent vertical light transmission per meter for several lakes in the ELA. Note the differences in the wavelength of maximum transmission among the lakes.

(< 10 ha) deeper than 4–5 m are thermally stratified for at least a part of the summer. Those with a maximum depth of 5–10 m usually have hypolimnia that are well above 4 C in summer. The hypolimnia of lakes with areas less than 5 ha and depths greater than 10 m usually remain very close to 4 C because of strong thermal stratification and reduced light penetration (all of these lakes are at least moderately humic). Larger lakes (500–1000 ha) must be at least 20 m in depth to have well-defined thermoclines; for example, on August 6, 1968, the thermocline in lake 161 (1007 ha) was at 13 m, and the temperature at 50 m was 5.7 C, indicating that heat transport (probably due both to wind and to radiation, since the waters are nearly colorless) to deeper strata was much greater than in the small lakes, as would be expected.

Small lakes shallower than 4–5 m have thermal properties ranging from unstratified to polymictic.[3] Most lakes in the area are dimictic, but some of the deeper small lakes may not mix completely if the period of spring or fall overturn is short.

All ELA lakes are covered with ice for a period of 5½–6½ months. Maximum ice thickness usually reaches only 0.5–1.0 m, since insulation by heavy snow cover inhibits the further formation of ice. (Windswept prairie lakes exposed to similar winter temperature regimes often have 1.5 to nearly 2 m of ice). Winter heat budgets for ELA lakes probably vary by a factor of two to three times, depending on winter air temperatures and snowfall in any given year, since the melting of ice accounts for the major portion of the winter heat income. There was no correlation between lake size and total thickness of ice cover, and local variations in snowfall and drifting of snow by the wind were probably more important. In the fall of 1968, for example, ice formed rapidly when there was little or no snow cover, but after heavy December and January snowfalls, it increased very little in thickness until a period of warm weather in March melted the snow on the ice. The ensuing cold weather after the March snowmelt added several centimeters of ice to the total cover.

Of particular interest in terms of experiments on the nutrient enrichment of entire lakes is the fact that midsummer epilimnion temperatures and summer heat incomes are comparable with those of continental European lakes at much more southerly latitudes, as well as to those of many of the world's north temperate lakes (Fig. 6*a–h* and Table 2; Hutchinson 1957 table 53). The period of highest temperatures is relatively short, however, lasting less than 1 month in 1968 and 1969. The winter heat income of ELA lakes is very high in all instances; for very shallow lakes it may equal or even exceed the summer heat income.

Gorham (1964), working with heat budgets of 71 lakes selected from the literature, demonstrated that lake area, volume, and mean depth all had important effects upon the annual heat budget. None of his regression equations gave good predictions for ELA lakes, although the same three morphometric parameters appeared to control annual heat budgets. Instead of logarithmic functions of $\bar{z}$, $\sqrt{A_o}$, and $\sqrt[3]{V}$ as used by Gorham, the best fits for regressions on annual heat budgets in ELA lakes were obtained by the equations[4]:

$$\text{Ⓗ}_{ba} = 5.88 + 1.17\ \bar{z} \qquad r^2 = 0.70 \qquad (4)$$

$$\text{Ⓗ}_{ba} = 9.63 + 0.19\ A_o \qquad r^2 = 0.69 \qquad (5)$$

$$\text{Ⓗ}_{ba} = 10.25 + 0.16\ V \qquad r^2 = 0.66 \qquad (6)$$

All values of r^2 are significant at the 1% level.

In the above calculations Ⓗ_{ba} is the annual heat income as defined by Hutchinson (1957) in kcal/cm^2, $\bar{z}$ is the mean depth in meters, A_o is surface area

[3]This term is applied by Hutchinson (1957) and Hutchinson and Löffler (1956) to high-altitude lakes in equatorial regions, where lakes may stratify by heating during the day, then mix completely during nighttime cooling. The same phenomenon occurs in many shallow north temperate lakes, and there appears to be no good reason why the term should not be applied, even though the lakes are at relatively low altitude.

[4]One must keep in mind that the independent variables are intercorrelated. For the 11 ELA lakes treated here, $r^2_{AV} = 0.80$, $r^2_{V\bar{z}} = 0.73$, $r^2_{A\bar{z}} = 0.57$ (all significant at 1%).

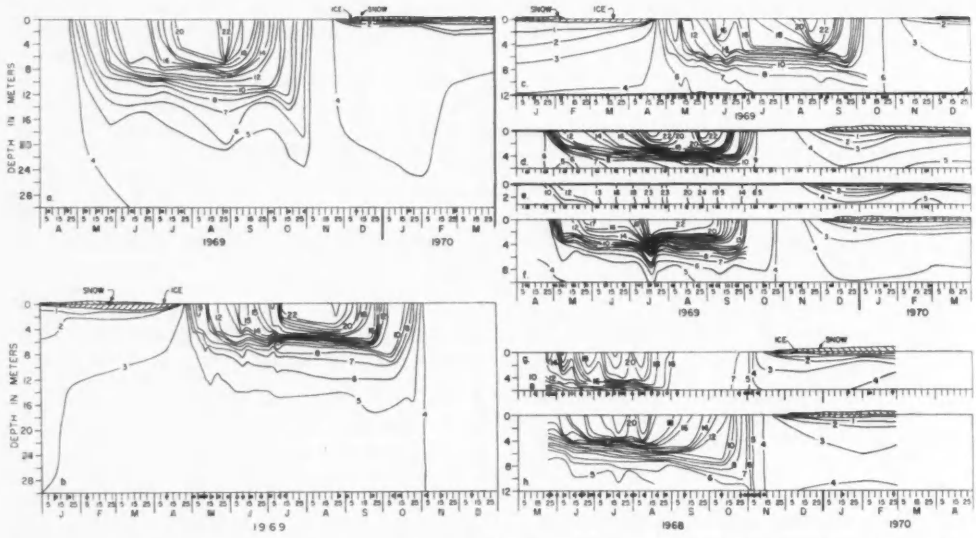

FIG. 6. Maps of seasonal isotherms for several ELA lakes: (*a*) lake 305, 1969–70; (*b*) lake 239, 1969; (*c*) lake 240, 1969; (*d*) lake 304, 1969–70; (*e*) lake 303, 1969–70; (*f*) lake 227, 1969–70; (*g*) lake 132, 1968 and 1970; (*h*) lake 122, 1968 and 1970. An asterisk (*) indicates dates of temperature measurements.

TABLE 2. Heat budgets for a variety of ELA lakes. The procedure and notation outlined by Hutchinson (1957) are used. Winter values include the melting of ice.

Lake	Year	$\bar{z}$ (*m*)	A_o (*ha*)	Summer $Ⓗ_{bs}$	Winter $Ⓗ_{bw}$	Total cal/cm² $Ⓗ_{ba}$
122	1968–69	7.2	12.2	8600	6300	14900
132	"	3.3	7.2	5500	6100	11600
227	"	4.4	5.0	6300	6200	12500
230	1969–70	6.2	1.7	6000	4700	10700
239	1968–69	10.5	56.1	10100	8200	18300
240	"	6.1	44.1	8900	5200	14100
241	"	5.5	1.8	3700	4700	8400[a]
302	1969–70	5.4	23.7	7850	–	–
303	1968–69	1.5	9.9	3200	4800	8000
304	"	3.2	3.6	5200	4500	9700
305	"	15.1	52.0	16000	8200	24200

[a]Only mixolimnion is considered.

in hectares, and V is volume in $10^5 m^3$. The difference from Gorham's calculations may be due to the fact that ELA lakes studied tend to be small, shallow, and close together, whereas his treatment included lakes of all latitudes, sizes, and elevations. Data for ELA lakes are given in Fig. 7*a–c*. In Fig. 7*a*, data from Hutchinson's (1957) table 53 are included, though not used in the calculation of regression. The plot includes only lakes with $\bar{z} < 25$ m. In general, Scandinavian lakes and those from northern continental Europe fit the ELA regression line quite well, whereas lakes from the British Isles and European Alps were slightly lower than predicted by regression, and Central America lakes were far lower. Large, shallow north temperate lakes (Lake Mendota,

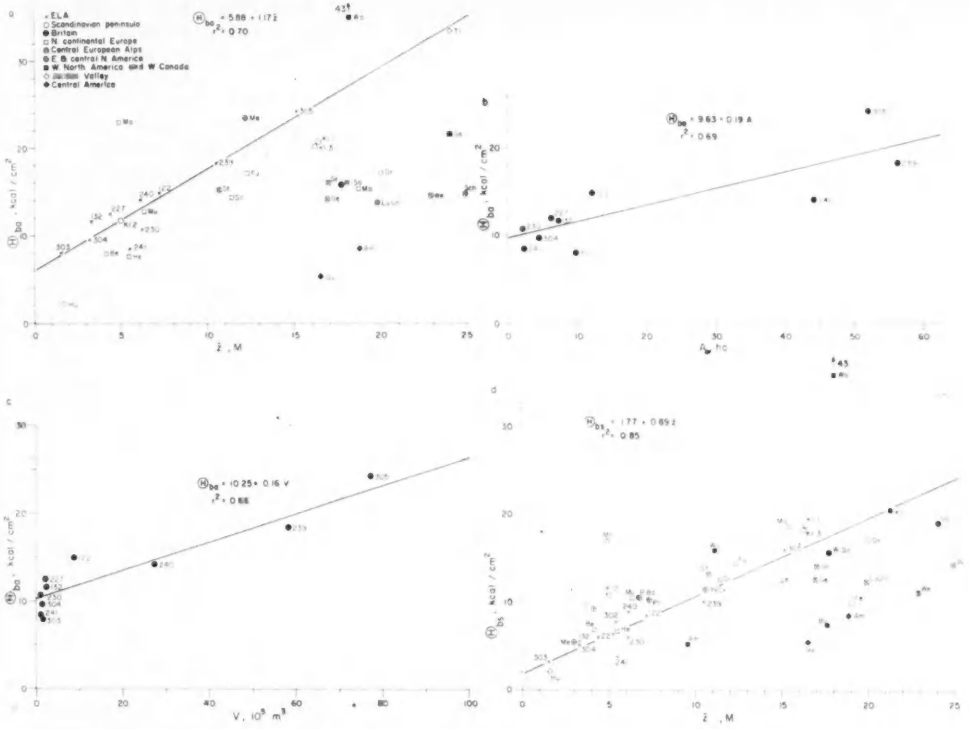

FIG. 7. Relation between morphometric parameters and annual heat budget ($\textcircled{H}_{ba}$) or summer heat income ($\textcircled{H}_{bs}$). Equations and symbols are given in the text. The regression line is calculated from ELA lakes only (numbered points). Other data shown in panels *a* and *d* are from Hutchinson's (1957) table 53. The first two letters of each lake name are used as a symbol for each point.

Lake Washington) had heat budgets higher than predicted. Israeli lakes fit the line well, a fact that is difficult to explain.

No similar comparisons were possible for area or volume, since the ELA lakes have far lower areas and volumes than any given by Hutchinson.

A better relation was observed between mean depth ($\bar{z}$) and summer heat income ($\textcircled{H}_{bs}$) than between $\bar{z}$ and $\textcircled{H}_{ba}$. The equation

$$\textcircled{H}_{bs} = 1.77 + 0.89\,\bar{z} \qquad (7)$$

fits the data well, with $r^2 = 0.85$. The same improvement was found using data for lakes with $\bar{z} < 25$ m. Including Hutchinson's shallow lakes plus ELA lakes in one calculation (Fig. 7*d*) gives:

$$r^2_{\bar{z}} = 0.23 \text{ for } \textcircled{H}_{ba}$$

$$r^2_{\bar{z}} = 0.36 \text{ for } \textcircled{H}_{bs}.$$

Both values are significant at the 1% level.

Work of the Wind and the Depth of the Thermocline

Birgean wind work (Birge 1916; see also Hutchinson 1957 p. 508) was calculated for ELA lakes with the belief that the inefficiency of heating for small shallow lakes mentioned by Hutchinson (1957 p. 509) would be demonstrated. As one may see from Table 3, this belief is erroneous, and small lakes are more efficiently heated than large ones. The column $B/\textcircled{H}_{bs}$ as calculated by Hutchinson cannot be considered as a measure of efficiency. The reciprocal, $\textcircled{H}_{bs}/B$, is, however, a true efficiency, since heat income depends upon wind work rather than vice versa. As one may see from Table 3, the small (1.7–56 ha) ELA lakes have a broad range of $B/\textcircled{H}_{bs}$,[5] with lower values

[5]Given as calculated by Hutchinson to facilitate comparison.

TABLE 3. Birgean wind work (B), wind work per unit summer heat income ($B/\textcircled{H}_{bs}$), and the efficiency of wind work ($\textcircled{H}_{bs}/B$) for ELA lakes. Depths and areas of lakes are given in Table 2. See text for discussion of the efficiency of wind work.

Lake	Year	B (*g cm/cm²*)	$B/\textcircled{H}_{bs}$ (*g cm/cal*)	$\textcircled{H}_{bs}/B$ (*cal/g cm*)
122	1968	689	0.080	12.5
132	"	206	0.037	27.0
227	1969	252	0.040	25.0
230	1969	387	0.064	15.6
239	"	1110	0.110	9.1
240	"	622	0.070	14.3
241	"	240[a]	0.065[a]	15.4
302	1968	296	0.038	26.3
303	1969	66	0.021	47.6
304	"	202	0.039	25.6
305	"	2425	0.152	6.6

[a]Mixolimnion only.

(and therefore higher efficiencies) for shallow lakes ($B/\textcircled{H}_{bs}$ from Hutchinson's table 58 ranges from 0.030 to 0.177 cal/g cm, whereas ELA lakes range from 0.021 to 0.152). According to Hutchinson (1957 p. 509) "the low value of $B/\textcircled{H}_{bs}$ (in small shallow lakes) is doubtless due to the loss, by evaporation and back-radiation at high surface temperatures, of a greater proportion of the heat that has been gained than is the case in an ordinary first-class lake." Although this statement is undoubtedly a correct observation on the utilization of wind work for heat distribution in very shallow lakes, it cannot be invoked as a general explanation for variation in $B/\textcircled{H}_{bs}$, since both B and $\textcircled{H}_{bs}$ are calculated from heat content of a lake *uncorrected* for evaporation and back-radiation.

There are several possible explanations for the more efficient heating of shallow lakes. The epilimnions of such lakes are usually a few degrees warmer than nearby deep lakes on the same date, due to radiant heating, so that the resulting lower density and viscosity of epilimnion waters may allow more efficient mixing of the epilimnion with overlying warm air during day light hours, when winds are generally much stronger than at night. Part of the work attributed to the wind in the Birgean calculation may actually be performed by inverse density currents induced by radiative warming of water in contact with the lake bottom in littoral regions.[6] At the sediment–water interface in shallow water extremely localized temperature gradients must develop on sunny days, resulting in the transfer of heat by ascending convection cells. As the proportion of littoral zone is larger in shallow lakes, a larger proportion of the total work in distributing the heat may be done by such currents.

Contrary to situations that have been described for other lakes, the wind does not move the thermocline of ELA lakes downward at all during the period when summer heat income is calculated. Instead, the depth of the thermocline is established early in the season, after which it remains at rather constant depth until well after the lake reaches maximum heat content. Figure 8*a* shows the depth of the thermocline in 1969 and part of 1970 for several ELA lakes. The depth of the thermocline in any year appears to be determined in the early part of the heating season by a combination of temperature and wind velocity. Note, for example, the shallow depth of the thermocline in lakes 227, 239, 240, and 304 in 1970, as compared with 1969. In 1970 the lakes stratified during a week of hot (30 C) still weather. Surface temperature gradients of 10 C/m were found in small shallow lakes. Figure 8*b* shows the maximum density difference per meter of depth in several ELA lakes in 1969 and early 1970. Temperatures profiles for two representative lakes during the week of hot still weather in 1970 are shown in Fig. 9, in comparison with 1969 values. The shallow thermoclines in 1970 were maintained by the strong density gradient, and the depth of the thermocline had not increased at all by early July, in spite of relatively strong winds and cool rainy weather in the latter two weeks of June. The heat budgets of ELA lakes therefore appear to be regulated by: (1) the depth of the thermocline as determined by spring meteorological conditions, plus (2) the maximum temperature of the epilimnion, which closely follows the maximum air temperature (Fig. 8*c*). There appears to be no correlation between thermocline depth and water color, and such a relation would be difficult to prove, since small lakes, which are more protected, are also usually more humic.

Other than its role in setting the initial position of the thermocline, the wind affects summer heat income very little in ELA lakes. Even when the thermocline begins to move downward in the fall, increased wind velocity does not appear to be a factor. Average wind velocity in the area is quite constant during the ice-free season, and 1969 was typical in this respect (Fig. 8*b* and *d*). The thermocline began to move downward within a few weeks after the lakes reached maximum heat content, in spite of density differences across the thermo-

[6]I am indebted to Dr J. R. Vallentyne for this suggestion. We have actually measured temperature inversions of several hundredths of a degree in shallow waters of lake 239 on hot sunny days.

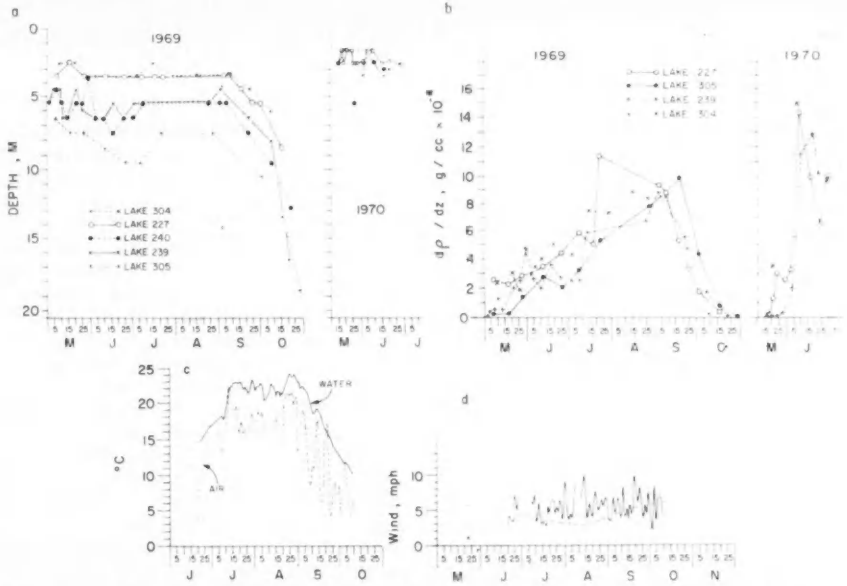

FIG. 8. (*a*) Depth of the thermocline (defined as maximum $d\theta/dz$ in the water column) in several ELA lakes, 1969. The apparent fluctuation in thermocline depth early in the season is the result of the formation of secondary thermoclines; the maximum value of $d\theta/dz$ is given in all instances. The small insert gives thermocline depths early in 1970, when the thermocline remained higher in the water column than in 1969. (*b*) Maximum change in density of lake water ($d\rho/dz$) over 1 m in several ELA lakes, 1969. The small insert shows the much greater density differences, and hence greater stabilities, that maintained the shallow thermoclines in 1970, as shown in 8*a*. (*c*) Air and epilimnion temperatures, lake 239, 1969. All values shown are the daily averages of measurements made at 10-min intervals from the tower mentioned above. The epilimnion temperatures are at a depth of 1 m; air temperatures are 1 m above the water surface. (*d*) Wind velocity. The solid line shows the daily average measurements recorded automatically 2 m above the surface of lake 239, 1969 (anemometer mounted on tower at the center of the lake). The broken line shows 15-year monthly averages for Kenora, Ont.

cline that were higher than those that proved stable in spring. This may be due to an increasing role by descending density currents, which are set up at the interface with overlying cooler air during the fall.

In view of the above facts, the calculation of heating efficiency in terms of "wind" work from the parameters $\textcircled{H}_{bs}$ and B should be viewed with great suspicion.

Oxygen

The azide modification of the Winkler technique was used for all measurements (American Public Health Association 1965).

The small lakes of 5–13 m depth that were described above as being subject to some hypolimnetic warming had anaerobic or nearly anaerobic hypolimnetic waters by late summer. Some of the deeper small lakes accumulated oxygen deficits for 2 or more years due to incomplete vernal or autumnal mixing, or both (Fig. 10*a–d*).

Many small, clear ELA lakes showed metalimnetic or hypolimnetic oxygen maxima in excess of those expected due to temperature change alone. These occurred only when accompanied by a shallow thermocline and Secchi disc visibility exceeding 5 m, even though nutrient, chlorophyll, and primary production data indicated that the lakes were oligotrophic (for example, Fig. 10*e*). Schindler and Nighswander (1970) showed similar data for Clear Lake in eastern Ontario. The phenomenon is lacking in lakes where the euphotic zone lies entirely within the epilimnion (Fig. 10*f*).

Shallow, unstratified or polymictic lakes were, of course, nearly saturated with oxygen all summer,

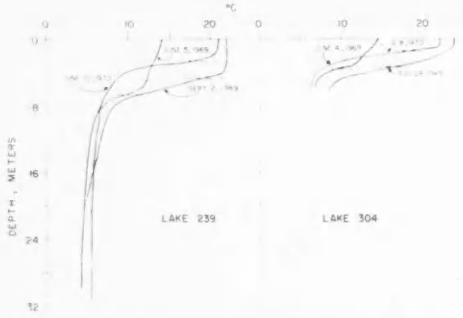

FIG. 9. Representative temperature profiles from two typical ELA lakes, 1969 and 1970. Values given are for the hot still week early in 1970, for the same period in 1969, and for late summer 1969. The position of the thermocline is shown by broken horizontal lines. Note the difference in thermocline depth in the 2 years, and the similar position of the thermocline for the two dates in 1969.

since in such unproductive waters (Schindler 1971; Schindler and Holmgren 1971) the nocturnal oxygen demand is low (Fig. 10*g–h*). Such lakes normally show higher oxygen depletion per m^3 under ice than do deeper lakes.

Most ELA lakes show considerable supersaturation with oxygen just under the ice in early winter. At least part of this may be due to phytoplankton production under clear ice early in the winter (Schindler 1971), since the oxygen concentrations are too high to be accounted for by freezing out of the gas alone, even if this were 100% efficient, which seems unlikely judging by the data of Mortimer (1941, 1942).

Most ELA lakes are humic, polymictic, or homothermal, or have phytoplankton production in the hypolimnion, factors that make the comparison of summer hypolimnetic oxygen deficits difficult to interpret. Of perhaps greater utility for comparing the magnitude of decomposition in such lakes, at least on a regional basis, is the rate of winter oxygen depletion. All ELA lakes are subjected to roughly similar covers of ice and snow, which minimize complications attributable to photosynthesis, mixing, or thermal differences. Hutchinson (1957 p. 641–642) discussed the difficulties in comparing summer oxygen deficits of lakes of different morphometry, and recommended calculating the mean of the deficits at several depths. This procedure is unnecessary if the morphometry of the lakes is known. An equivalent basis for comparing lakes may be obtained by estimating

$$W = \frac{1}{V(t_2 - t_1)} \int_{z=o}^{z=z_m} A_z \, (C_{zt_1} - C_{zt_2}) \, dz, \qquad (8)$$

where A_z is the area of the lake at depth z, C_{zt_1} and C_{zt_2} are oxygen concentrations at depth z and times t_1 and t_2, and V is the volume of the lake. The integral can be conveniently evaluated planimetrically. The result gives average oxygen depletion per unit volume per unit time (W) (Table 4).

Rates of oxygen depletion under ice permit comparisons among lakes of different trophy, or of variations in different years, that are relatively independent of climatic factors. Unfortunately, lakes without winter ice cover or those that have high winter photosynthesis due to insufficient snow cover cannot be compared in this way. Severson Lake, Minnesota (Schindler unpublished data) is included in Table 4, since in contrast to ELA lakes it is highly productive.

None of the oxygen values given in Table 4 is corrected for the increase in oxygen under ice expected as the result of freezing out and no measurements were made of the oxygen content of ice in this study. Mortimer (1941, 1942) found that the oxygen content of ice from Esthwaite water varied greatly, from 35 to 68% saturation, with

TABLE 4. Rates of oxygen depletion under ice in several ELA lakes. A hypereutrophic lake is included for comparison.

Lake	Period (*days*)	Year	(W) mg $O_2/m^3 \cdot day$	mg $O_2/m^2 \cdot day$ avg
122	77	1969–70	35.2	253
132	69	1968–69	39.7	131
132	77	1969–70	27.7	91
227	53	1968–69	46.3	204
227	79	1969–70	54.8	241
230	34	1970	22.3	138
239	64	1968–69	15.0	158
239	78	1969–70	20.4	214
240	59	1968–69	30.9	188
240	76	1969–70	34.3	209
261	35	1970	15.6	45
265	34	1970	17.4	171
303	75	1969–70	23.8	36
304	75	1969–70	73.8	236
305	27	1968–69	13.4	202
305	75	1969–70	13.7	207
Severson L.[a]	48	1964–65	80.8	178

[a]Highly eutrophic Minnesota lake (Schindler unpublished data).

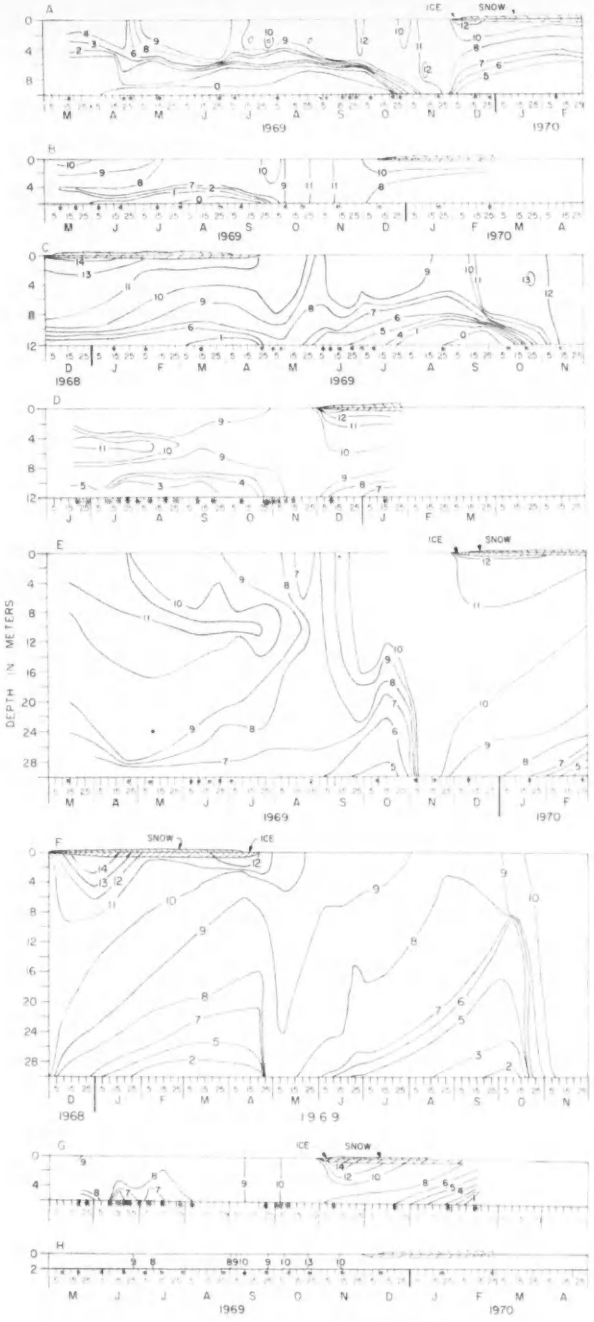

FIG. 10. Seasonal oxygen isopleths for several ELA lakes: (A) lake 227; (B) lake 304; (C) lake 240; (D) lake 122; (E) lake 305; (F) lake 239; (G) lake 132; (H) lake 303. An asterisk (*) indicates dates of sampling.

higher concentrations from cloudy layers of ice containing bubbles. Since much of the ice in ELA lakes is formed above rather than below the original early winter ice surface, due to water seeping through cracks in the ice under the weight of snowfalls, a correction for freezing out would be difficult to calculate. If one assumes a 50% freeze out of oxygen, the calculated oxygen consumption of lake 303 could be nearly 10% low. The error would be less in other lakes.

A great variety of combinations of thermal and oxygen regimes exist within ELA (Table 5),

TABLE 5. Temperature and oxygen characteristics of near-bottom waters for selected ELA lakes, 1968.

Lake	Date	Depth at station (*m*)	Sample depth (*m*)	O_2 (*ppm*)	Bottom temp (*C*)	Stratification[a]
8	Aug. 12	11.5	10.1	0.04	5.9	II
67	15	10.8	10.0	0	5.0	II
69	15	5.7	5.0	0	9.2	II
70	15	3.5	2.0	7.95	16.8	III
81	14	7.0	5.5	0.1	4.3	I
82	14	4.0	2.0	6.48	16.3	III
95	9	5.3	4.0	0.01	5.8	II
99	9	5.8	5.0	3.4	9.2	III
114	July 6	2.5	1.0	8.2	12.3	III
120	Nov. 13	19.8	19.0	0	5.0	Meromictic, dichothermic
122	July 25	11.8	10.0	4.0	4.1	I
127	Aug. 7	3.1	3.0	7.0	18.2	III
132	July 24	6.3	5.0	6.3	10.1	III
149	Aug. 14	4.2	2.0	8.5	15.4	III
150	14	7.3	6.0	0	9.8	II
162	9	3.8	3.0	8.5	15.1	III
163	8	8.5	8.0	1.2	8.7	II
164	8	6.6	6.0	0.1	8.0	II
165	8	4.1	3.0	6.3	16.0	III
189	7	14.0	13.0	0.2	5.6	II
227	July 5	10.0	9.0	0.1	4.4	II occasional incomplete mixing
230	5	13.6	12.0	0.1	4.0	I occasional incomplete mixing
239	5	30.4	30.0	4.1	4.8	I–II
240	5	13.1	10.0	5.9	7.3	II
241	5	12.5	11.0	0	4.9	I–II meromictic, dichothermic
251	Aug. 15	15.0	14.0	4.5	6.6	I–II
253	15	2.8	2.0	8.2	17.2	III
254	6	21.2	20.0	7.4	6.0	I–II
256	9	21.2	20.0	5.8	6.6	I–II
257	9	5.8	5.0	1.5	11.8	II–III
261	July 6	9.7	9.0	0.1	5.7	II
265	July 6	18.4	17.0	3.8	4.0	I
269	Aug. 7	3.0	2.0	0.8	16.6	II–III
302	July 6	14.0	13.0	0.1	5.3	I–II
303	6	2.5	2.0	8.2	14.3	III
304	5	5.4	5.0	7.0	8.3	III
305	5	30.0	25.0	7.8	4.8	I
(Hillock) 161	Aug. 6	117.0	116.0	8.8	4.1	I
(Mad Dog) 465	7	30.0	23.0	5.5	5.1	I–II
(Highwind) 464	6	35.0	35.0	9.4	5.3	I–II

[a]Thermal classification of Hutchinson (1957).

making the area nearly ideal for experimental purposes from this standpoint.

Acknowledgments

R. K. Lane kindly supplied pyrheliometer data and meteorological data from lake 239 and the spectroradiometer for this study. F. A. J. Armstrong and analytical laboratory staff did many of the oxygen measurements. J. Shearer and J. Johnson made several of the light and temperature measurements in 1969; J. Gray and P. Campbell measured temperatures and took samples for oxygen on many occasions in 1968. G. J. Brunskill, E. Gorham, G. D. Koshinsky, K. Patalas, and J. R. Vallentyne made many helpful suggestions on the manuscript.

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Preliminary Chemical Characterization of Waters in the Experimental Lakes Area, Northwestern Ontario[1]

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Water analyses in 1968 and 1969 from 40 small lakes within a small area of the Canadian Shield in northwestern Ontario gave mean values for Ca, Na, Mg, and K of 1.6, 0.9, 0.9, and 0.4 mg/liter with Ca > Na > Mg > K on a molar basis. HCO_3, SO_4, and Cl (on a smaller number of samples) were 4.1, 3.0, and 1.4 mg/liter. Total CO_2 was variable in the range 0.3–12.0 mg/liter. Specific conductance was in the range 10–35 μmho/cm at 25 C and *p*H 5.4–7.5. Color was <5–150 Hazen units, and plant pigments (as chlorophyll *a*) <1–21 μg/liter. Total dissolved nitrogen was in the range 110–300 mg N/liter and total dissolved phosphorus 3–20 μg P/liter. NO_3-N and PO_4-P were often undetectable in summer, and reached winter maxima around 100 and 10 μg/liter.

Total dissolved nitrogen and phosphorus contents of five lakes were computed at the beginning and end of periods of several weeks during summer stagnation. Changes were negligibly small in three of the deeper lakes, but the two shallowest showed increases of 0.22 and 0.62 g N/m² and 0.03 and 0.13 g P/m². Analyses of precipitation and stream waters were used, with stream flow rates, to calculate input and output of nutrients from four of these lakes during the same periods. Retention of nutrients had occurred in all, and it was concluded that in the two deeper lakes nutrients had been lost to the sediments, whereas in the two shallower ones the increases in dissolved nutrients found were derived from the sediments.

Analyses of 33 other Canadian Shield lake areas and of 13 other dilute lakes in other regions are tabulated. Comparison with the Experimental Lakes Area (ELA) lakes shows that the latter are more dilute than any in the Shield area except for some in the Northwest Territories, and much more dilute than any others in the world except for some alpine lakes in California.

Received August 5, 1970

PRELIMINARY chemical investigations (reviewed by Johnson and Vallentyne 1971) of the waters in the Experimental Lakes Area (ELA) were designed to provide basic survey information about the area so that similarities and differences in the chemical composition of lakes of different sizes, morphometry, and color could be discerned as a preliminary to the planning of artificial enrichment studies. The same information allowed the average chemical composition of ELA lakes to be compared with that of other lake districts of the world, and provided a background for interpretation of biological differences among the areas (which are revealed by biological survey work). Later work, done chiefly in 1969, was designed to examine seasonal changes in the chemical composition of various types of lakes and factors responsible for them, mainly to obtain the detailed chemical information necessary for proper interpretation of postfertilization changes in water chemistry.

Methods

1968 SURVEY

Samples were taken from 40 lakes in the area, chosen from the 465 lakes surveyed in 1967 on the basis of size, depth, transparency, and accessibility. Most of these were within ½ mile of logging roads and could be reached by two men carrying limnological equipment and a light canoe. Others were several miles from the nearest road and were reached by helicopter. To obtain samples from the same locations during the surveys, from one to three permanent buoys were placed in each lake, depending on its size. At least one of these was near the area of maximum depth (z_m). Three sets of samples

[1]The fifth in a series of 14 papers on the work of the Fisheries Research Board of Canada, describing background environmental data on the Experimental Lakes Area, northwestern Ontario. For location of numbered lakes see insert map at the back of this issue of the Journal of the Fisheries Research Board of Canada. A key to lake locations is given by Cleugh and Hauser (1971).

Printed in Canada (J1877)

were taken, the first in May–June, a second in July–August, and a third in October–November.

Water samples were taken with a Van Dorn sampler for chemical analysis, and with 1-inch diam tygon tube for chlorophyll, phytoplankton, and rotifer samples (Lund and Talling 1957). Van Dorn samples were taken at depths of 1 m, just above and just below the thermocline, and at 1 m above the bottom. Three 500-cc polyethylene bottles were rinsed and filled for chemical analysis from each depth and a 300-cc Biological Oxygen Demand bottle was filled and fixed for oxygen measurement. Phytoplankton and rotifers from mixed tube samples were preserved in acid Lugol's solution, and a third portion from the tube sample was kept for chlorophyll analysis. Tube samples for phytoplankton and chlorophyll were taken to 2× Secchi disc visibility, representing the euphotic zone, and the tube was lowered to the bottom of the lake (or to the maximum tube length of 20 m in deeper lakes) for rotifer samples. Other measurements made on the same date were temperature profiles, Secchi disc visibility, general weather observations, and zooplankton hauls with a modified Clarke-Bumpus net (described by Patalas 1971).

1969 Sampling

Six lakes were sampled at 1- to 2-week intervals, and several others from three to six times during the year. Samples were taken with a Van Dorn sampler at 1 m, 5 m, and at 5-m intervals, the lowest being taken at 1 m above the bottom. Chlorophyll, phytoplankton, and primary production samples were taken at seven intervals in the euphotic zone, with additional samples for CO_2 determination by gas chromatography (Schindler and Holmgren 1971). Temperature, light penetration, and Secchi disc visibility measurements (Schindler 1971) were also co-ordinated with the chemical sampling program.

A 2 × 2-m precipitation collector was set up on the western shore of lake 239. Samples from it were analyzed after each rainfall. In addition, occasional samples were analyzed from runoff streams in the basins of lakes 239 and 240, and from the outflows of lakes 239, 240, 303, and 227. Only general results of all sampling programs will be presented here; detailed information will be presented at a later date.

Analysis

Oxygen was determined by the azide modification of the Winkler method in Standard Methods (American Public Health Association 1965) as soon as possible after collection. In 1968 one polyethylene bottle from each depth was frozen and kept at –10 to –20 C. These were later thawed, mixed, and specific conductance determined. Unfiltered samples were used for analysis for calcium, magnesium, sodium, and potassium by atomic absorption spectrophotometry. It has since been found that the freezing causes somewhat erratic results in these analyses, and for this reason individual analyses are unreliable. It appears, however, that the means of several analyses come close to values found on unfrozen samples. The results in the table are average values and have been supported by later analyses. The effect of freezing samples for silica was more serious, frozen samples yielding results much lower than unfrozen ones, as reported by Kobayashi (1967).

A second sample was filtered soon after collection (Whatman GF/C glass fiber filter), frozen, and kept at low temperature. This sample was thawed and mixed just before analysis for nitrate (by reduction to nitrite, Wood et al. 1967), phosphate (Murphy and Riley 1962), and for total dissolved nitrogen (TDN) and total dissolved phosphorus (TDP) after ultraviolet photochemical combustion (Armstrong and Tibbitts 1968). The photooxidation also made possible a determination of total dissolved iron in some waters. For this, samples were made 0.0005 N with HCl before irradiation, so that iron remained in solution and could be determined absorptiometrically with 1:10 phenanthroline (Armstrong 1957).

A third sample of 500 cc was filtered for chlorophyll *a* determination using a 4.25-cm diam Whatman GF/C filter and $MgCO_3$. Concentrations were measured absorptiometrically and calculated (as chlorophyll *a* uncorrected for phaeophytin) by the equations of Strickland and Parsons (1965).

The color of filtered samples from the October–November survey was measured in a visual color comparator (Tintometer Company) by comparison with glass disc standards in Hazen units.

In 1969, analyses for NH_4-N, NO_2-N, NO_3-N, TDN, PO_4-P, TDP, SiO_2-Si, and chlorophyll *a* were done in the field laboratory and the need to freeze samples was avoided.

Ammonium nitrogen was determined by the phenol-hypochlorite method of Solórzano (1969), nitrite by the procedure of Bendschneider and Robinson (1952), and silicate by a molybdenum blue method (Armstrong and Butler 1962). Ammonia and nitrite determinations were started as soon as possible after collection of samples. This was usually within 3 hr but for more distant lakes was within 6 hr. Suspended matter was separated by filtration of about 500 cc of sample on a previously ignited Whatman GF/C filter; this was then dried in a desiccator over silica gel and stored at –10 to –20 until analyzed. The filter was cut in half to give equal portions of the collected suspended matter. Carbon and nitrogen in one half were determined with a Perkin-Elmer Model 240 Elemental Analyzer, and phosphorus in the other by a spectrophotometric molybdenum blue method, after ignition at low temperature and acid extraction. Some experimental details, notes on blank determinations, and tests of the method are given elsewhere (Stockner and Armstrong 1971).

Chlorophyll *a* was determined by the fluorimetric procedure after extraction by 90% acetone with the aid of a tissue grinder (Yentsch and Menzel 1963). The fluorometer was standardized with acetone extracts of phytoplankton from the upper layers of the 10 lakes listed in Table 3. Agreement between the two instruments

was good ($r^2 = 0.98$). Spectrophotometric measurements on these extracts were also made and chlorophyll *a* calculated by using the parameters of Strickland and Parsons (1965). The fractions of plant pigments present as chlorophyll *a* and as phaeophytins or phaeophorbides is uncertain (Yentsch and Menzel 1963; Strickland and Parsons 1965).

Chloride and sulfate were determined by the mercuric nitrate and barium sulfate methods (American Public Health Association 1965).

Results and Discussion

Average Composition of ELA Waters

Averages of the three 1968 determinations from each lake are given in Table 1. Temperature, oxygen, and light data from the surveys are reported by Schindler (1971) and crustacean zooplankton by Patalas (1971). Analyses of rotifer and phytoplankton samples are not complete.

Table 1. Averaged analyses from the euphotic zones of ELA lakes, 1968.

Lake	Sp. cond.[a] (μmho/cm at 25 C)	mg/liter				Total cations (meq/liter)	Fe (mg/liter)	mg/liter				Ratio, TDS:sp. cond.	Color (Hazen units)
		Ca	Mg	Na	K			Tot. diss.[a] N	Tot. diss. P	Chlorophyll *a* μg/liter	Chlorophyll *a* mg/m²		
8	16	1.4	0.9	0.6	0.3	0.178	0.02	180	13	3–9	24–72	2.1	10
67	22	1.5	0.9	0.9	0.5	0.202	0.1	240	6	2–3	8–12	0.9	45
69	22	2.2	1.1	1.0	0.5	0.258	0.05	200	8	1–8	2–12	1.1	55
70	25	2.3	1.1	0.9	0.7	0.263	0.1	240	14	5–15	17–50	0.7	65
81	20	1.3	1.0	0.7	0.6	0.194	0.1	200	5	6–21	18–60	1.4	90
82	40	4.4	1.1	1.0	0.8	0.376	0.02	300	9	4–9	5–11	1.2	110
95	22	1.8	0.9	1.1	0.5	0.226	0.1	160	10	2–5	3–8	1.7	140
99	20	1.4	1.0	0.8	0.5	0.201	0.05	220	8	3–6	12–24	0.75	25
114	14	1.0	0.9	0.5	0.3	0.154	0.05	150	5	1–3	4–13	0.52	18
122	16	1.5	0.8	0.7	0.3	0.179	0.02	150	8	1–5	8–40	2.18	18
127	15	1.1	0.7	0.6	0.3	0.147	0.02	200	5	1–3	5–8	1.43	20
132	15	1.2	0.9	0.6	0.3	0.168	0.02	150	5	1–3	9–25	1.00	15
149	26	2.2	0.9	1.1	0.5	0.246	0.01	280	10	3	15	0.3	18
150	32	3.0	1.0	1.3	0.6	0.305	0.02	300	7	2–4	8–16	0.60	25
152	24	1.8	0.9	1.2	0.6	0.233	0.05	240	13	2–6	12–36	0.38	20
161	25	2.2	0.9	0.9	0.5	0.237	0.02	150	7	1–3	17–50	0.71	5
162	17	1.8	0.7	0.7	0.3	0.186	0.02	180	9	4–9	20–45	1.73	18
163	26	3.0	1.0	1.2	0.6	0.201	0.02	180	8	3–6	15–30	1.42	15
164	17	1.5	0.9	0.8	0.3	0.192	0.05	150	6	2–4	8–16	2.38	50
165	18	1.5	1.1	0.8	0.3	0.208	0.05	150	6	1–3	4–12	1.36	35
189	20	1.8	0.9	1.0	0.4	0.218	0.02	160	7	4–7	32–56	1.36	10
227	18	1.7	1.0	0.8	0.2	0.207	0.05	160	7	2–5	9–22	2.85	18
230	15	1.3	0.8	0.7	0.4	0.172	0.01	180	8	3–12	17–65	2.66	25
239	22	1.9	1.3	1.1	0.5	0.263	0.05	160	6	1–2	7–14	0.80	20
240	20	2.0	1.0	0.9	0.4	0.232	0.05	150	5	2	7	0.90	25
241	20	1.2	1.1	1.0	0.5	0.208	0.02	160	4	2–4	7–14	0.55	65
251	32	3.0	1.5	1.2	0.7	0.345	0.1	150	8	2–3	14–21	2.64	12
253	22	2.1	0.9	1.0	0.5	0.236	0.05	250	20	3–5	12–20	1.92	45
254	28	2.4	1.0	1.0	0.5	0.259	0.01	120	5	2	20	1.87	10
256	24	2.2	0.9	0.8	0.4	0.230	0.01	110	9	1	12	1.25	5
527	16	1.2	0.7	0.8	0.3	0.160	0.1	150	8	1–3	3–9	1.11	50
261	15	1.1	0.7	0.7	0.2	0.148	0.05	120	3	1–2	6–12	1.66	25
265	22	1.9	1.0	1.1	0.5	0.239	0.02	140	4	2–3	14–21	2.00	12
269	20	1.8	1.0	1.0	0.5	0.229	0.1	200	5	4–6	12–18	1.00	80
302	15	1.5	0.8	0.6	0.3	0.175	0.05	140	6	2–3	18–27	2.63	15
303	12	0.9	0.6	0.5	0.2	0.121	0.02	130	5	1–2	8–16	2.94	12
304	14	1.1	0.7	0.5	0.2	0.140	0.1	150	6	1	3	2.50	20
305	22	2.2	0.9	0.8	0.4	0.230	0.02	150	5	1	11	0.83	8
464	27	2.3	1.1	1.0	0.5	0.262	0.02	130	8	1–2	9–18	–	18
465	26	2.3	0.9	1.1	0.5	0.250	0.05	150	5	1–2	8–16	–	12

[a]Sp. cond., specific conductivity; tot. diss., total dissolved.

The lakes are very similar in chemical composition. Major cation concentrations are extremely low, with Ca > Na > Mg > K (on a molar basis) in most surface waters. There is good correlation between total concentration of cations and specific conductivity (Fig. 1). Summary data are set out in Table 2.

The lakes are low in nutrients compared with many well-studied lakes of the world; this is discussed below. Dissolved orthophosphate was not usually detectable in summer, being less than 1 µg PO_4-P/liter except occasionally in hypolimnetic water. In winter some samples from a few of the more accessible lakes showed concentrations around 10 µg PO_4-P/liter. Throughout the year total dissolved phosphorus was 5–20 µg P/liter.

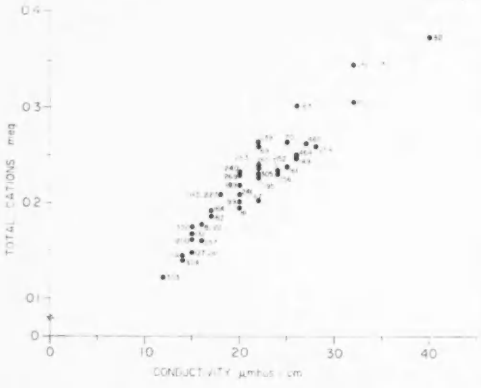

FIG. 1. Relation between specific conductance (µmho/cm at 25 C) and total cation concentration (mg/liter) for numbered ELA lakes.

Nitrate also was low in summer, seldom exceeding 10 µg NO_3-N/liter, but increasing in winter to 100 µg NO_3-N/liter in the upper layers of some lakes. In the oxygen-deficient hypolimnions of small deep lakes, nitrogen was found as ammonia in concentrations up to 1000 µg NH_4-N/liter or more. Total dissolved nitrogen in surface waters was 100–300 µg N/liter at all times. N:P ratios in surface waters were from 12:1 to 40:1 by weight.

Average concentrations of plant pigments in the euphotic zones of all lakes were very low (Table 2), except on one date when a few lakes showed what might (amongst Canadian Shield lakes only) be termed weak phytoplankton blooms.

Table 3 gives an idea of year-to-year variation in several ions, by comparing analyses from the euphotic zones of several lakes in mid-June of 1968 with similar samples from June 1969. Although most differences are of only a few percent, some ions, in particular phosphate and nitrate, show much greater differences. Judging by the seasonal changes observed in 1969 these differences between the 2 years, in nutrient concentrations, cannot be explained in terms only of seasonal variations of either ion, and we do not place much reliance on nutrient analyses for intercomparisons between lakes.

TABLE 2. Other chemical data for euphotic zone of ELA lakes 1968–69. Means, medians, or modes are not given when these numbers are meaningless.

	No. lakes	Range	Mean	Median	Mode
Specific conductance (*µmho/cm at 25 C*)	463	11–161	–	21	–
Calcium (*mg Ca/liter*)	40	0.6–4.5	1.6	1.8	1.8
Magnesium (*mg Mg/liter*)	40	0.5–2.4	0.9	0.9	0.9
Sodium (*mg Na/liter*)	40	0.4–1.7	0.9	0.9	1.0
Potassium (*mg K/liter*)	40	0.2–1.0	0.4	0.5	0.5
Chloride (*mg Cl/liter*)	7	0.6–4.2	1.4	1.4	0.8
Sulphate (*mg SO_4/liter*)	7	0.6–5.0	3.0	2.5	3.4
Bicarbonate (*mg HCO_3/liter*)	12	0.15–9.9	4.1	4.0	4.6
Total CO_2 (*mg CO_2/liter*)	18	0.26–12.0	–	–	–
*p*H	15	5.4–7.5	–	–	–
Total dissolved nitrogen (*µg N/liter*)	40	110–300	177	160	150
Total dissolved phosphorus (*µg P/liter*)	40	3–20	7	7	5
Total dissolved iron (*µg Fe/liter*)	40	10–100	50	50	20
Chlorophyll *a* (*µg/liter*)	40	<1–21	3	3	2
Color (*Hazen units*)	40	<5–150	32	20	18

TABLE 3. Partial analysis of 1-m water samples from 10 ELA lakes, June 1968 and June 1969.

Lake		TDN (μg/liter)	TDP (μg/liter)	NO_3-N (μg N/liter)	PO_4-P (μg P/liter)	mg/liter Ca	Mg	Na	K	As chlorophyll *a* (μg/liter)
99	1968	195	4	40	<1	1.36	–	0.86	0.60	–
	1969	168	6	35	4	1.30	0.48	0.83	0.49	2.7
227	1968	–	–	8	<1	1.65	–	0.87	0.38	2.2
	1969	144	3	<1	2	1.85	0.70	0.90	0.23	2.2
230	1968	–	–	4	<1	0.88	–	0.60	0.34	9.6
	1969	121	3	4	1	0.82	0.58	0.68	0.41	1.6
239	1968	–	–	4	<1	2.03	–	1.06	0.47	–
	1969	143	4	24	3	2.15	0.79	1.16	0.50	2.7
240	1968	–	–	<1	<1	1.61	–	0.87	0.36	0.8
	1969	201	2	6	1	1.73	0.64	0.80	0.30	1.9
241	1968	–	–	2	<1	0.89	–	0.70	0.39	–
	1969	117	–	2	–	1.25	0.80	0.67	0.52	–
302	1968	–	–	<1	<1	1.34	–	0.50	0.32	1.6
	1969	164	4	7	6	1.30	0.53	0.62	0.33	2.7
303	1968	–	–	2	<1	0.89	–	0.54	0.28	1.6
	1969	106	8	<1	1	1.15	0.51	0.59	0.12	2.4
304	1968	–	–	<1	<1	1.09	–	0.54	0.21	4.0
	1969	167	8	38	1	1.05	0.50	0.74	0.12	5.9
305	1968	–	–	24	<1	1.95	–	0.74	0.34	0.6
	1969	116	4	<1	2	2.06	0.69	0.94	0.34	1.3

SEASONAL CHANGES IN IONIC CONCENTRATIONS OF ELA WATERS

There are considerable seasonal and lake-to-lake variations in the distribution and abundance of both nutrient and major ions (Fig. 2, 3). These patterns are likely to be a function of biological activity in the water column and of two separate factors: (1) external sources of nutrients, namely surface run-off, groundwater, and precipitation; (2) internal sources of nutrients, i.e. return of ions from sediments. For convenience we will examine these factors separately.

(1) *External sources of nitrogen, phosphorus, and major cations*

Analyses of precipitation and surface runoff samples revealed that both must be considered to be sources of nutrients for ELA lakes. An average of 26 samples taken during the ice-free season from the two inflow streams to lake 239 (neither of which drain other lakes (see insert map)) showed TDN concentrations nearly twice as great as in samples from the outlet of the lake; TDP in inflow streams was 1.5 times as high as in the outflow streams. Similar results were found for other lakes in the area. Seven samples of rain and 20 of snow gave average values for dissolved nitrogen and phosphorus much higher than the concentrations in the lakes. The data are set out in Table 4. Flow rates are being measured (Newbury and Cherry 1970) along with these chemical analyses and it should be possible later to calculate nitrogen and phosphorus budgets for several lakes.

That surface runoff samples are lower in dissolved nitrogen and phosphorus than rainfall is undoubtedly due to uptake by terrestrial vegetation. Bormann et al. (1968) and Schindler and Nighswander (1970) report similar findings. We do not have sufficiently detailed data at present.

Concentrations of major cations in surface runoff water should be higher than in precipitation because of decomposition and solution processes in soils, glacial drift minerals, and exposed bedrock (Likens et al. 1967; Johnson et al. 1968; Schindler and Nighswander 1970; Brunskill et al. 1971). Surface runoff analyses are available from the drainage to lakes 239 and 240. Two streams enter lake 239, both consisting entirely of surface flow and groundwater, i.e., there are no permanent water bodies higher in either drainage basin (see insert map). Lake 240 also receives surface water from two streams: one the outlet from lake 239, the other from a stream draining lakes 303, 304, 470, and 661. Table 5 gives average concentrations of major cations from these systems.

The eastern inflow to lake 239 contains higher concentrations of all major ions than either lake

or outflow waters. The northwest inlet to the lake is, however, low in concentration, representing a diluent for all major cations in the lake. Although the difference is to some extent expected, since the eastern drainage basin has twice the area of the other and sediments in the basin are thicker and

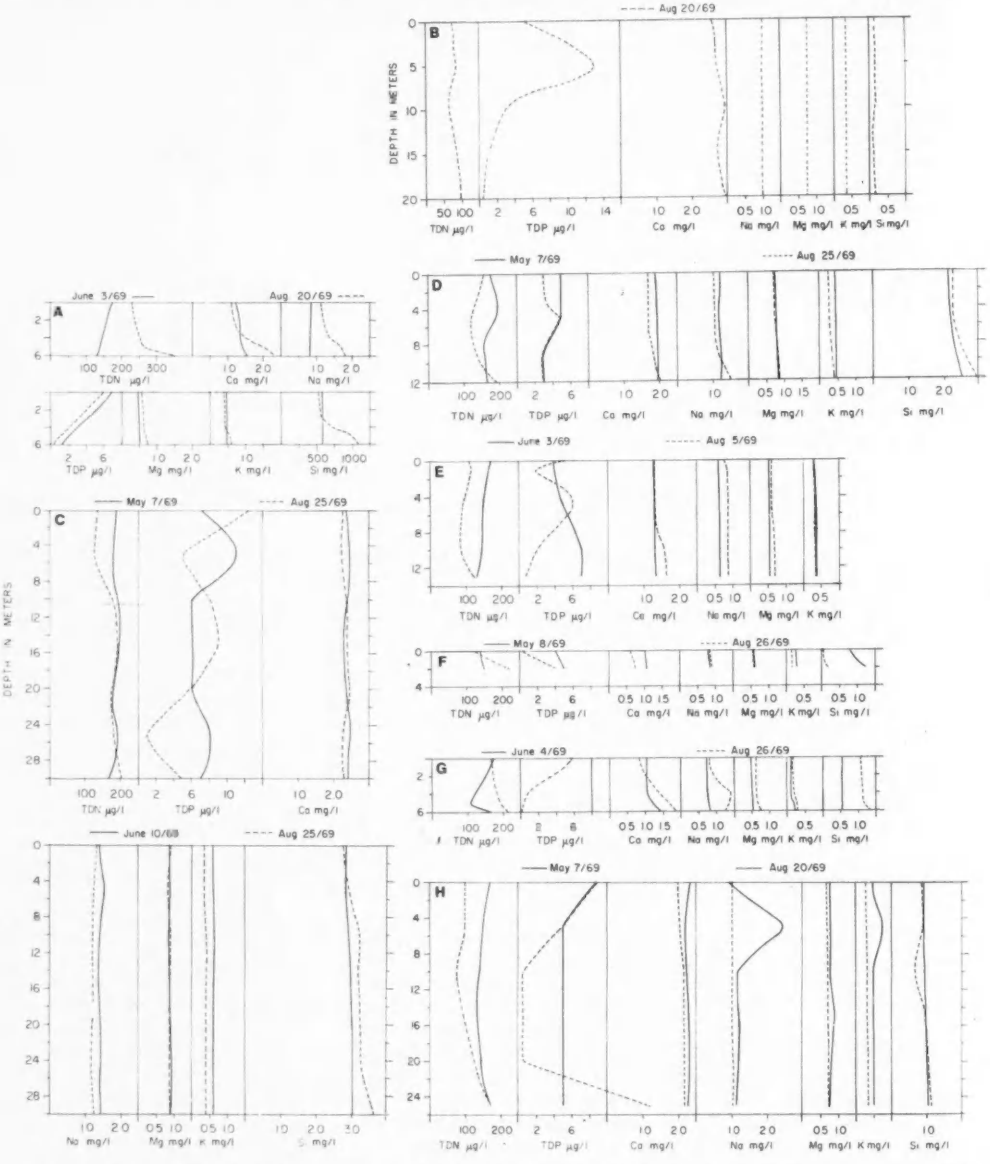

FIG. 2. Vertical distribution in summer for chemical constituents of ELA lakes. Total dissolved nitrogen (TDN) and total dissolved phosphorus (TDP) in µg N or P/liter, other elements in mg/liter. A, lake 99; B, 161; C, 239; D, 240; E, 302; F, 303; G, 304; H, 305.

more varied, hydrological data are necessary for more detailed interpretation. The western inflow stream to lake 240, which drains four other lakes, is also more dilute than the water of that lake. Direct precipitation in the ELA is very low in major cations, and the proportions of these differ from those in the lake waters. The eastern inflow stream is probably the primary surface source of cations to lake 239 and the outflow from lake 239 is in turn the major surface source of cations to lake 240.

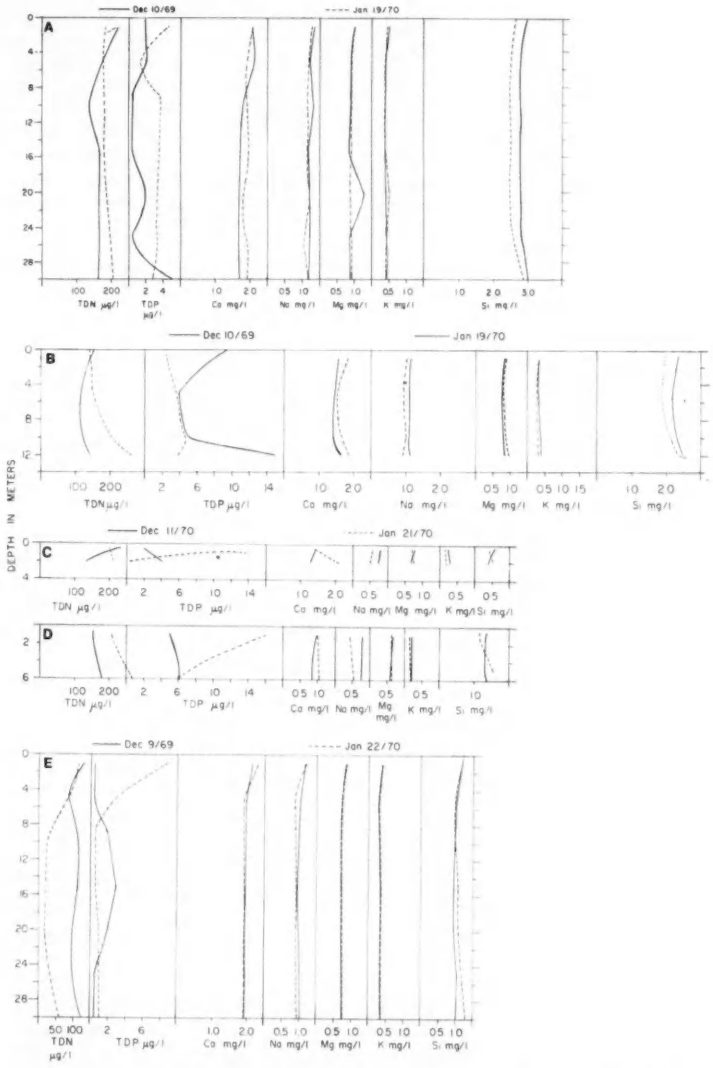

FIG. 3. Vertical distribution in winter for chemical constituents of ELA lakes, total dissolved nitrogen (TDN) and total dissolved phosphorus (TDP) in µg N or P/liter, other elements in mg/liter. A, lake 239; B, 240; C, 303; D, 304; E, 305.

TABLE 4. Total dissolved nitrogen and phosphorus (μg/liter) in streams and precipitation in ELA, 1968–70. Number of samples analyzed is given in parentheses.

	Range	Tot. diss. N	Range	Tot. diss. P
Inflow streams to lake 239	123–430	198(26)	1–99	6.4(26)
Rain } Lake 239		378(7)		18(7)
Snow } basin	220–496	368(20)	4–28	9.5(11)
Outflow of lake 239	18–155	109(13)	<0.1–11	4.6(13)

TABLE 5. Average dissolved major cations (mg/liter) of streams and precipitation in ELA, 1968–70. Locations of streams are shown on the insert map.

	No. analyses	Ca	Mg	Na	K
L. 239, E inflow stream	13	2.46	0.96	1.47	0.58
L. 239, NW inflow stream	13	1.30	0.59	0.83	0.21
L. 239, outflow (=inflow to lake 240)	12	2.12	0.80	1.13	0.50
L. 240, W inflow stream	11	1.14	0.57	0.75	0.20
L. 240, outlet	11	1.59	0.64	1.06	0.36
Rain	2	<0.10	0.10	0.22	0.09
Snow	8	0.26	0.04	0.20	0.10

(2) *Release of nutrient elements from sediments, and the effect of biological activity in the water column*

In the study of eutrophication processes, the possibility of nutrients being released from sediments after being precipitated is important, since their return may supplement external nutrient supplies and encourage nuisance growths of algae. It is possible that the release of nutrients from sediments would also prolong the recovery time of culturally eutrophied lakes, once the artificial external sources of nutrients are removed.

Evidence in the literature concerning nutrient release from sediments is contradictory. Einsele (1936), Mortimer (1941, 1942), and Schindler and Comita (1971) found appreciable feedback of nutrients from anaerobic sediments, but Ahl (1966) found that nitrogen, though not phosphorus, was returned from the sediments of shallow Lake Ösbysjön. Vollenweider (1969) did not find enough substantial evidence on sediментary release of nutrients to include it as a parameter in his eutrophication model. The matter is discussed in more detail by Hutchinson (1957).

The above authors did not include data on external sources of nutrients or lake outflow, so that it is impossible to evaluate their conclusions, since one cannot tell whether the observed increases in hypolimnetic nutrient concentrations were the result of decomposition of organic material formed during the year of study, or of decomposition of previously laid down sedimentary matter. Any dissolved inorganic nutrient entering the water column, either from the sediments or from external sources, is likely to be quickly assimilated by plankton, so that increases in nutrient concentrations in the water column appear in the suspended, rather than the dissolved component (see Fig. 4, 5; also

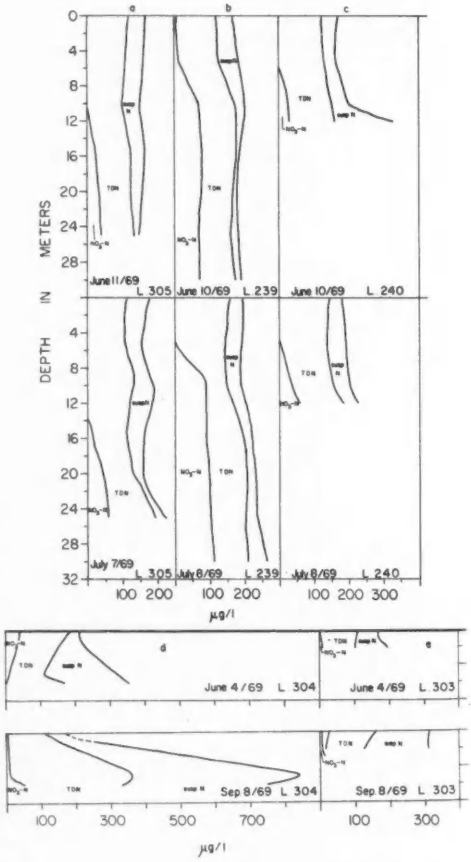

FIG. 4. Vertical distribution of nitrogen components (μg N/liter) in ELA lakes 1969.

Schindler et al. unpublished data). To provide conclusive results it is necessary to monitor concentrations of all fractions of nutrients (inorganic and organic, dissolved and suspended) in the water column, as well as external sources of nutrients (precipitation, stream flow, and groundwater),

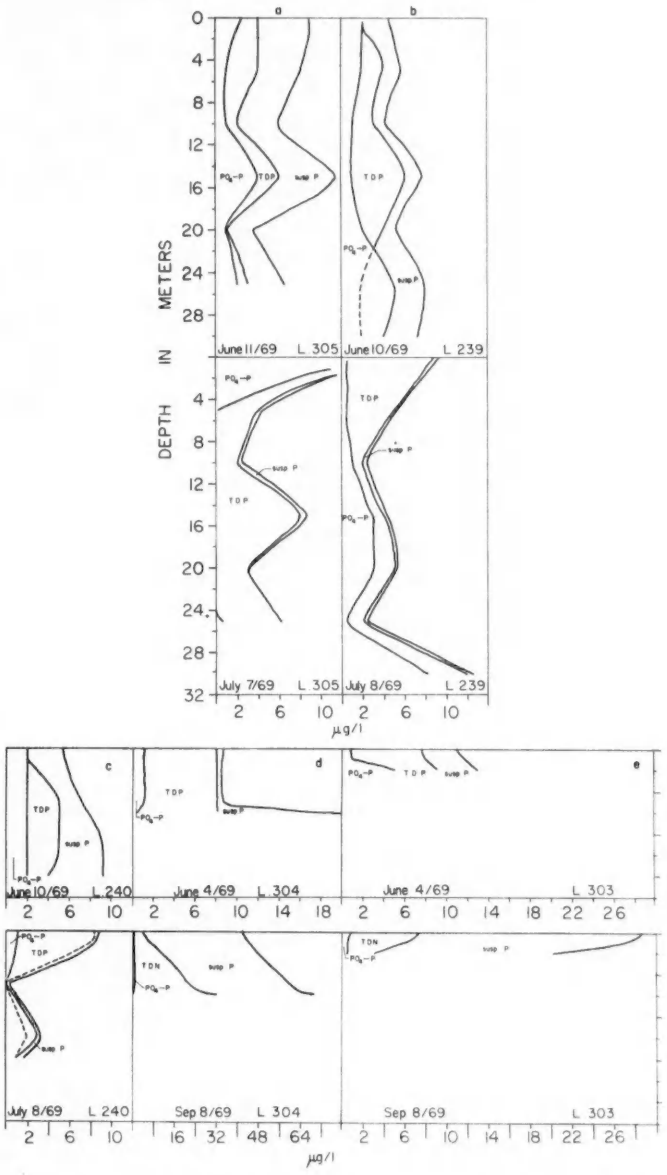

FIG. 5. Vertical distribution of phosphorus components (µg P/liter) in ELA lakes, 1969.

TABLE 6. Measured increases in total (dissolved + particulate) nitrogen and phosphorus in ELA lake water masses during summer stagnation.

Lake	Period	Nitrogen		Phosphorus	
		kg	*g/m²*	*kg*	*g/m²*
239	June 10–July 8	Negligible	0	Negligible	0
240	"	"	0	"	0
303	June 4–Sept. 8	22.0	0.22	2.6	0.026
304	"	22.3	0.62	4.8	0.132
305	June 11–July 7	Negligible	0	Negligible	0

and outflow of nutrients from the lake. Volumes of precipitation, stream and groundwater flow, evaporation and evapotranspiration, outflow, lake morphometry, and drainage area must also be known.

We have been able to make preliminary calculations for four lakes for the summer of 1969. N and P profiles for lakes 239, 240, 303, 304, and 305 are shown in Fig. 4 and 5 as mentioned above. (The drainage system of lake 240 is complicated and this lake was not included in the calculations that follow.) It may be seen that in the summer N and P concentrations increased in the water columns of lakes 303 and 304, but that there was little change in lakes 239, 240, and 305. The change in the total quantity of N and P in a lake is obtained from the expression:

$$M_c = \int_{z=0}^{z=z_m} A_z\,[(C_{zt_2}) - (C_{zt_1})]\,dz \qquad (1)$$

where M_c = the increase in total mass of the nutrient in the lake, z_m = maximum depth, A_z = area at depth z, and (C_{zt_1}) and (C_{zt_2}) are concentrations at depth z and times t_1 and t_2. Results of calculations for four lakes are given in Table 6.

We have assumed that nutrient concentrations in the runoff reaching all lakes were the same as in lake 239. Nutrient inputs and outflows were obtained from the equations:

$$M_1 = \sum_{t_1}^{t_2} \left\{(A_o)\,(P)\,(C_p) + A_d\,(P - E_t)(C_r)\right\} \qquad (2)$$

$$M_2 = \sum_{t_1}^{t_2} C_o \left\{(A_o)\,(P - E) + A_d\,(P - E_t)\right\} \qquad (3)$$

where M_1 and M_2 are the masses of nutrient inflow and outflow during the period t_1 to t_2; P, E, and E_t are precipitation, evaporation, and evapotranspiration (Newbury and Cherry 1970), A_o and A_d are surface areas of lake and terrestrial drainage area, and C_p, C_r, and C_o are concentrations of nutrients in precipitation, runoff, and outflow. Results of calculations are shown in Tables 7 and 8.

The excess of N and P in input over that in outflow in lakes 239 and 305 does not appear as an increase in the dissolved or suspended components of the water mass, and must have been lost to the sediments (see Fig. 4*a*, *b* and 5*a*, *b*). On the other hand, the increased quantities of N and P in the water of lakes 303 and 304 (Table 6) are not, apparently, supplied entirely from external sources

TABLE 7. Inputs of nitrogen and phosphorus to four ELA lakes during the period as in Table 6.

Lake	Streams (*kg*)		Precipitation (*kg*)		Total (M_1) (*kg*)	
	N	P	N	P	N	P
239	5.4	0.22	18.2	0.87	23.6	1.09
303	19.8	0.99	14.8	0.70	34.6	1.69
304	13.4	0.40	5.4	0.26	18.8	0.66
305	3.2	0.32	15.9	0.76	19.1	1.08

TABLE 8. Outflow and net retention (runoff + ppt − outflow) of nitrogen and phosphorus in four ELA lakes in the same summer period as in Tables 6 and 7.

Lake	Outflow (streams) (*kg*)		Net retention			
			kg		% of supply	
	N	P	N	P	N	P
239	5.6	0.23	18.0	0.86	76	79
303	22.6	1.13	12.0	0.56	35	33
304	14.6	0.44	4.2	0.22	22	33
305	3.5	0.35	15.6	0.73	82	68

and are very probably derived from the sediments (see Fig. 4*c*, *d* and 5*c*, *d*).[2]

Table 9 shows the exchange between water column and sediments. The apparent return of nutrients from the sediments in the two shallow ELA lakes had little to do with oxygen regimes, since lake 304 had an anaerobic hypolimnion throughout the period of observation, and lake 303, having no hypolimnion at all, should have had an oxidized mud–water interface. The differences in period of calculation for the four lakes do not affect results. The major differences may be related to morphometry, since lakes 303 and 304 are much shallower than 239 and 305 ($\bar{z}$ = 1.5, 3.2, 10.5, and 15.1 m for lakes 303, 304, 239, and 305, respectively) or to the ratio of sediment area to volume (surface area to volume, A_o/V = 6.62, 3.15, 0.95, and 0.66 for lakes 303, 304, 239, and 305, respectively). The sediments of all lakes were similar in texture and chiefly organic in nature, although those of the shallower lakes were higher in carbon, nitrogen, and phosphorus (Brunskill et al. 1971).

Ionic Composition of Other Dilute Waters

A considerable body of chemical data exists for lakes in the Canadian Shield, some of it in our own files, or in publications or reports where it is not readily available. We have therefore summarized it in Table 10, to show how ELA compares with other lakes of the Canadian Shield. Absolute reliance must not be put on data in all instances, since many analyses represent a single sample from each lake and analytical methods are not known for all publications. Data for anions are questionable, since the usual acid titration method for the CO_2 system is nearly impossible in the more dilute lakes (Schindler and Holmgren 1971; Schindler and Nighswander 1970). Sulfate and chloride, too, are near or below the limit of detectability of most commonly used methods in many regions. The problem is further complicated by the fact that silicate, ammonia, and the hydrogen ion, all of which show great seasonal variation, are in many instances major components of total ionic concentration.

Even though the exact intercomparability of major ion data is questionable, several trends are apparent from the data. ELA lakes are the most dilute known in the Canadian Shield, with the exception of the large lakes in the Northwest Territories (Mackay, Snowbird, Angikuni, Casmir, Nueltin, Nonacho, and Obre lakes, which are widely separated). This observation is based upon conductivity measurements, which are probably the most reliable basis for comparison. The ions of coastal Shield lakes (Nova Scotia and Newfoundland) are dominated by Na and Cl because of their proximity to the sea (Gorham 1957a, b). With the exception of Wollaston Lake and the eastern Ontario Group (Mg^{++} and $SO_4^{=}$ dominated) most Shield lake waters appear to be dominated by Ca^{++} and HCO_3^- (comparison on basis of ionic strength). This may be due to calcareous material in glacial drift in some areas, although glacial drifts of the ELA are mainly of silicate minerals (Brunskill et al. 1971). McLeod Bay and the eastern Ontario lakes, both in relatively well-scoured areas of the Shield have very little glacial drift of any type. Gorham (1957a) found bicarbonate to be

[2]One must use caution in making this conclusion, because of the assumption made concerning the concentration of N and P in runoff. If the actual C_p is in the range ½–2× of the values found for lake 239, as seems likely, sediments must have contributed to the nutrient budget of the lake. All runoff waters sampled in ELA are within this range.

TABLE 9. Calculated N and P exchange between water column and sediments in four ELA lakes during summer stagnation. Symbols are defined in the text. Negative values indicate sedimentation, positive values indicate "feedback" to the water column.

		$M_c-(M_I-M_o)$ (*kg*)		Nutrient exchange ($g/m^2 \cdot day^a$)		% total nutrient supply ($=M_c+M_I$) from sediments		% M_I lost to sediments	
Lake	Days	N	P	N	P	N	P	N	P
239	28	−18.0	−0.9	−1146	−57	–	–	76	79
303	96	10.0	2.0	1049	210	39	60	–	–
304	96	18.1	4.6	5208	1324	54	87	–	–
305	26	−15.6	−0.7	−1154	−52	–	–	82	68

[a]m^2 refers to lake surface area.

TABLE 10. Ionic composition of dilute waters (m

Ref. no.	Ca	Mg	Na	K	HCO_3	SO_4	Cl	Si	PO	NO_3-N
I. Canadian Shield										
1. Experimental Lakes Area, Ont.	1.6	0.9	0.9	0.4	3.8	3	1.4	0.5	<0.	0.02
2. Haliburton Highlands, Ont.	1.9	1.3	0.7	0.3	4.1	3.9	0.6	–	<0.	0.040
3. Ont., general	–	–	–	–	–	–	–	–		–
4. N Sask.	5.8	3.1	2.5	1.7	34.0	3.3	–	1.4		<0.06
5. Lac la Ronge area, Sask.	9.7	2.2	2.1	1.8	14.6	0	0	1.3		–
6. McLeod Bay, Gt. Slave L., NWT	2.8	1.4	0.8	0.4	11.6	0.8	0.5	0.3	<0.	0.050
7. Reindeer L.	2.5	1.3	1.8	1.1	15.3	2.0	0.3	2.0		0.6
8. Wollaston L., Sask.	2.6	1.8	0.4	2.5	23.6	5.8	0.4	0.2		0.06
9. Lynn L. area, Man.	3.4	1.0	1.0	0.5	11.1[a]	3.0	1.5	–		–
10. S of Gt. Slave, small lakes, NWT	7.8	2.7	2.7	1.1	30.0[a]	5.3	4.1	–		–
11. Large lakes, NWT	2.0	1.0	0.5	0.3	9.1[a]	<2	0.4	0.2		–
12. N.S. granite	1.1	0.5	5.0	0.4	Nil	6.2	7.5	–		–
13. N.S. gold-bearing	2.3	0.5	3.2	0.6	2.7	5.4	5.2			
14. Nfld.	2.0	0.3	3.1	0.2	4.9	2.6	4.8	0.4		–
15. NE Minn.	3.4[b]	1.1[b]	–	–	39.6	2.6	0.5	–		–
16. NE Wis.	5.1	2.5	1.0	1.5	9.3	4.0	1.0	2.2	0.	–
17. Cree L., Sask.	2.6	1.0	←5.8→		24.6	0.6	1.4	0.2		0.04
18. Eagle L., Ont.	6.6	2.0	3.2	1.7	29.3	5.1	1.2	0.9		1.2
19. Lac Seul (at Ear Falls)	11.0	2.2	2.2	1.4	42.5	5.8	1.0	1.2		0.1
20. Upper Gt. L. drainage	6.7	1.9	2.0	1.0	19.0	9.9	1.9	1.5		0.6
21. Ottawa R. drainage	7.4	2.1	←2.8→		21.3	10.2	0	2.4		1.9
22. L. Nipigon	23.3	3.9	1.5	0.7	86.7	3.8	1.6	3.6		0.3
23. L. Nipissing	8.8	2.5	←1.4→		3.4	10.3	0	5.9		3.1
II. Partial Shield Drainage										
24. Flin Flon area, Man.	22.3	14.9	5.7	1.6	–	26.5	4.3	1.2		–
25. L. Winnipeg, Man.	20	8.6	6.0	2.0	116	3.0	5.2	1.9	0.	0.330
26. Christy Bay, Gt. Slave L., NWT	16.7	7.2	5.0	1.5	76.2	32	8.5	1.4	0.	0.054
27. Gt. Bear L., NWT	16.2	6.9	4.2	0.8	68	14.8	4.8	2.2		0.8
28. L. of the Woods	14.6	3.6	0.9	0.4	53.7	6.0	3.3	2.9		0.02
29. L. Superior	12.4	2.8	1.1	0.6	28.1	3.2	1.9	2.1	0.	0.52
30. Sask. and Churchill drainage	26.4	12.1	←1.7→		123	5.7	4.0	2.0		–
31. 17 lakes, Sask.	12.9	3.5	2.1	1.9	50.5	Nil	Nil	1.0		–
32. Pelican-Deschambault lakes	14.2	5.3	3.5	<2.5–5	69.7	Nil	0.5	3.3		–
33. Nettilling L., Baffin Is.	1.6	1.4	←16.7→		40.2	4.4	1.4	4.2		0.13
34. S. Indian L., outlet	7.3	3.0	2.1	1.0	35.7	<1	2.2	0.9	0.	0.05
III. Other Dilute Lake Districts										
Adirondack Mts., N.Y.	2.4	0.6	←1.7→		5	5.7	0.7	–		0.33
New England	7.3	1.4	2.9	0.6	23.2	8.8	2.9	–		–
Colorado, alpine	3.7	–	–	–	–	–	–	–	0.	0.063
High Sierras, Calif.	0.6	0.04	0.6	–	–	–	–	0.9		–
Chile & Argentina	3.5	1.8	2.9	1.3	–	–	–	–		–
Alpine Peru	5.3	1.4	1.1	0.2	–	–	–	–		–
Karelian District, USSR	7.3	2.1	←2.4→		25.1	6.7	2.0	3.3		–
Malingsbo-Kloten, Sweden	4.0	0.7	1.7	0.8	8.3	7.8	2.7	2.0	0	0.025
W Ireland	4.0	1.0	8.6	0.5	8.9	5.2	14.7	–		–
Cairngorm area, Scotland	0.7	0.2	2.0	0.3	0.9	2.3	2.6	1.1	<0	0.04
Alpine Himalayas	–	–	–	–	–	0.1–4.3	<0.4	0.3–5.0	<0. 0	–
Alpine Mt. Kenya	~30	0.2	0.6–7.2	0.3–2.5	–	–	–	–		–
English L. District	4.5	1.0	3.9	0.5	7.8	6.3	7.1	–		0.8
World avg freshwater	15	4.1	6.3	2.3	58.4	11.2	7.8	6.0		–

[a]Calculated by difference.
[b]One analysis only.

ilute waters (mg/liter). (A dash (–) indicates no data.)

PO_4	NO_3-N	Tot. diss. P	Tot. diss. N	Tot. Fe	pH	TDS	Conduc. μmho/cm	No. lakes	Source
<0.0	0.02	0.007	0.177	0.05	5.6–6.7	33	19	40	Present study
<0.0	0.040	–	–	–	5.0–7.1	–	26	5	Schindler (unpub. data)
	–	–	–	–	–	65	–	310	Ryder 1964
	<0.06	–	–	–	7.4	54	60	5	Koshinsky 1965
	–	–	–	–	7.1	65	72	28	Koshinsky 1968
<0.0	0.050	0.3	–	–	7.2	22	28	1	Thomas 1957; Brunskill & Armstrong
	0.6	–	–	–	7.2	28	31	1	(unpub. data)
	0.06	–	–	0.005	7.0–7.3	35	35	1	Thomas 1957; Rawson 1959
	–	–	–	–	–	52	31	17	Armstrong & Patalas (unpub. data)
	–	–	–	–	–	54	–	9	
	–	<0.001	<0.125	0.01	–	10	20	7	
	–	–	–	–	4.7	–	–	10	Gorham 1957a
					5.7		40,32	9	
	–	0.020	<0.050	0.19	6.3–7.1	–	31	29	Kerekes MS 1968
	–	–	–	–	–	–	–	Not given	Moyle 1954
0.0	–	0.020	–	0.04	–	–	37	8–530	Juday et al. 1938; Juday & Birge 1931, 1933; Lohuis et al. 1938
	0.04	–	–	Nil	6.8–7.0	27	–	1	Rawson 1959
	1.2	–	–	0.01	7.3	–	68	1	Thomas 1959
	0.1	–	–	0.04	7.6	64	79	1	Thomas 1959
	0.6	–	–	0.8	6.1–8.2	59	63	18	Thomas 1965
	1.9	–	–	0.05	6.8–8.7	50	64	13	Thomas 1952
	0.3	–	–	0.10	7.8	108	149	1	Thomas 1965
	3.1	–	–	–	7.4	59	76	1	Thomas 1954
	–	0.012	0.43	0.01	–	185	242	16	Armstrong & Patalas (unpub. data)
0.0	0.330	–	–	–	8.0	150	205	1	Brunskill &
0.0	0.054	–	–	–	7.9	160	180	1	Armstrong (unpub. data)
	0.8	–	–	0.13	7.8	–	155	1	L. Johnson (unpub. data)
	0.02	–	–	0.15	7.8	100	111	1	Thomas 1959; Livingstone 1963
0.0	0.52	–	–	0.36	7.4	82	79	1	Beeton & Chandler 1962
	–	–	–	0.024	8.1–8.2	136	–	5 large	Rawson 1957; Thomas 1958
	–	–	–	–	7.4	93	94	17	Lane 1967
	–	–	–	–	6.9–8.6	98	109	4	Johnson 1967
	0.13	–	–	Nil	6.8–7.0	37	–	1	Oliver 1964
0.0	0.05	0.018	0.465	–	–	60	65	1	Armstrong & Hamilton (unpub. data)
	0.33	–	–	0.14	5.6	–	29	9	Berg 1963
	–	–	–	–	–	–	–	7	Brooks & Deevey 1963
0.0	0.063	–	–	–	6.9	–	–	19	Pennack 1963
	–	–	–	0.001	6.0	–	7	170	
	–	–	–	–	–	–	–	11–12	Löffler 1960
	–	–	–	–	–	–	–	5	Löffler 1960
	–	–	0.10	6.6–8.2		–	–	3–16	Baranov 1962
0.0	0.025	0.019	0.265	–	6.1	–	36	40	Ahl 1968
	–	–	–	–	6.6	–	–	6	Gorham 1957c
<0.0	0.04	–	–	–	5.7	–	–	7	Gorham 1957 b
<0.0	–	–	–	–	6.8–8.5	–	7–43	24	Löffler 1969
0.0									
	–	–	–	–	–	–	7–31	1–15	Löffler 1964
	0.8	–	–	–	–	–	–	12	Macan 1970
	–	–	–	0.67	–	–	–	–	Livingstone 1963

undetectable in Nova Scotia lakes in granite basins. Such low concentrations appear to be typical for small lakes in many areas of the Shield, including ELA and the Haliburton Highlands. Bicarbonate concentrations as low as 0.6 mg/liter have been found in surface waters of small ELA lakes in midsummer. Low concentrations appear to be caused by photosynthesis of phytoplankton (Schindler unpublished data).

The second category in Table 10 includes lakes on the edge of the Canadian Shield that drain soluble geological substrates as well as igneous rock. As would be expected, the effect upon ionic composition is dramatic in all instances, with the concentrations of Ca^{++} and HCO_3^- increasing markedly, so that total ionic concentrations are an order of magnitude higher than in waters that drain the Shield alone. The effect is similar in all instances, even though the examples represent a variety of soluble geological materials, including limestones and dolomites, conglomerate rock, basaltic areas, and glacial drift. Figure 6 shows the location of areas summarized in Table 10.

A third category in Table 10 lists other lake districts with dilute waters. Only waters of the alpine area of California studied by Bradford et al. (1968) are more dilute than ELA lakes, although the ionic concentrations of the Scottish lakes are very similar. Waters of the southern Schwarzwald (Elster 1955, 1957, 1959) and northern Sweden (Rodhe 1949) are also very dilute, though data are not presented in tabular form, so that direct comparisons are difficult. Slightly higher ionic concentrations in the other regions are in general due to higher levels of Ca^{++} and HCO_3^-.

Almost every major lake district of the world contains a few very dilute lakes, and a complete list of comparisons would be needlessly time consuming. The average ionic concentration of ELA lakes is lower than those of most thoroughly studied lake districts of the world, as well as that of a world average freshwater (see Table 10).

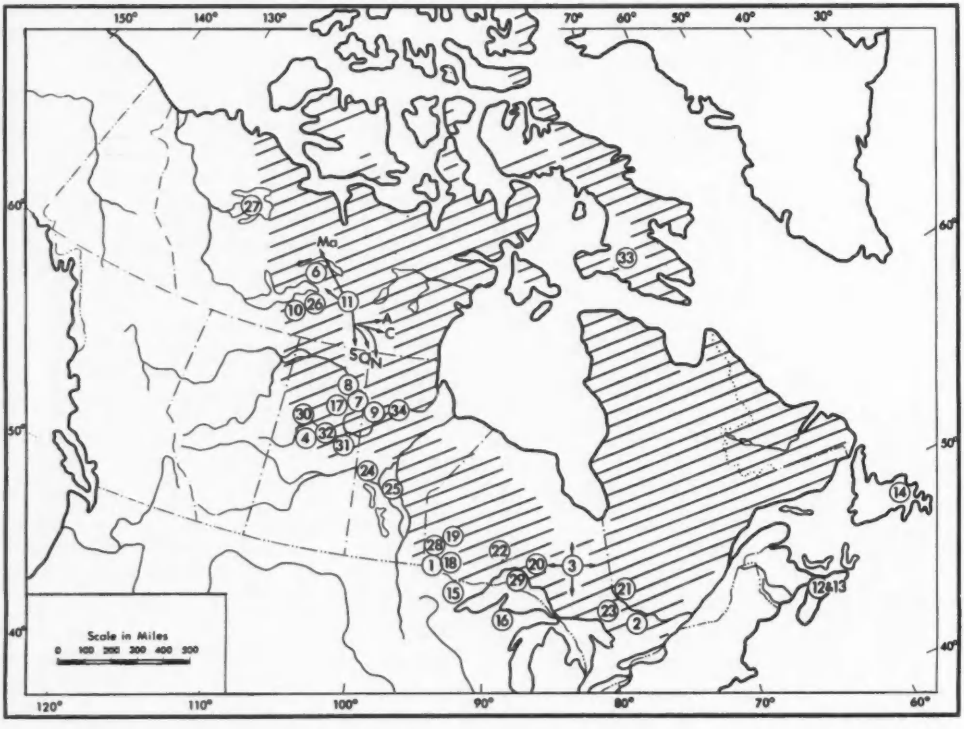

FIG. 6. Locations of lakes in Canadian Shield for which analyses are given in Table 10: Ma, Mackay Lake; O, Obre Lake; N, Nueltin Lake; C, Casmir Lake; A, Angikuni Lake; S, Snowbird Lake.

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Primary Production and Phytoplankton in the Experimental Lakes Area, Northwestern Ontario, and other Low-Carbonate Waters, and a Liquid Scintillation Method for Determining ^{14}C Activity in Photosynthesis[1]

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A modified ^{14}C method is described for measuring phytoplankton production in low-carbonate waters. The procedure includes the use of the Arthur and Rigler (Limnol. Oceanogr. 12: 121–124, 1967) technique for determining filtration error, liquid scintillation counting for determining the radioactivity of membrane filters and stock ^{14}C solutions, and gas chromatography for measuring total CO_2.

Primary production, chlorophyll *a*, and total CO_2 were measured for two dates in midsummer from each of several lakes in the Experimental Lakes Area (ELA), ranging from 1 to 1000 ha in area and from 2 to 117 m in maximum depth. Phytoplankton species abundance and biomass were determined for the same dates. Production ranged from 0.02 to 2.12 g C/m^3·day and from 0.179 to 1.103 g C/m^2·day. Chlorophyll ranged from 0.4 to 44 mg/m^3 and from 5 to 98 mg/m^2 in the euphotic zone. The corresponding ranges for live phytoplankton biomass were 120–5400 mg/m^3 and 2100–13,400 mg/m^2. Chrysophyceae dominated the phytoplankton of most of the lakes.

A system for classifying the lakes in terms of phytoplankton species composition and production–depth curves is developed.

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ALTHOUGH the Canadian Precambrian Shield contains the world's largest unbroken lake district, few publications have described the phytoplankton or primary production of Shield waters. The purpose of this paper is to report the range and general characteristics of phytoplankton standing crop and production values likely to be encountered in a variety of Shield lakes in the Experimental Lakes Area (ELA), and to outline some modifications of the ^{14}C technique that are useful or essential for determining phytoplankton production in Canadian Shield or other waters with low phytoplankton production and low ionic concentrations.

Some information about phytoplankton in the lakes at the extreme southwestern edge of the Canadian Shield is available in the work of Drouet (1954) and Meyer and Brook (1967, 1968, 1970). Both authors present annotated lists of phytoplankton species and notes on habitat. Unfortunately, they did not obtain information on primary production, cell biomass, or nutrient conditions. Several other papers have dealt with the net phytoplankton of large northern Shield lakes and Saskatchewan lakes (Rawson 1956, 1957, 1960a, b, 1961; Lund 1962). Koshinsky (MS 1964, 1965, MS 1968) also gives data for Saskatchewan lakes in the Shield. None of the above papers treats the phytoplankton community in a detailed quantitative manner. Recently Christie (1968, 1969) has studied the phytoplankton standing crop and limiting nutrients in several lakes in and near the Canadian Shield in eastern Ontario. Bourrelly (1966) has studied the taxonomy of algae from Quebec and eastern Ontario. Johnson et al. (1969), Schindler (1971a), and Schindler and Nighswander (1970, and unpublished data) give limited information on the phytoplankton biomass and productivity of lakes in eastern Ontario.

The data analyzed here consist of midsummer production and standing crop measurements from

[1]The sixth in a series of 14 papers on the work of the Fisheries Research Board of Canada, describing background environmental data on the Experimental Lakes Area, northwestern Ontario. For location of numbered lakes see insert map at the back of this issue of the Journal of the Fisheries Research Board of Canada. A key to lake locations is given by Cleugh and Hauser (1971).

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a variety of lakes. Results from two dates in midsummer were analyzed for each lake. Whenever possible one was a cloudless day and the other an overcast one. More complete seasonal changes in species abundance, phytoplankton biomass, and ^{14}C production in several lakes will be described at a later date.

Materials and Methods

Phytoplankton Production

Some problems were encountered with all commonly used methods for determining phytoplankton production.

The oxygen method proved too insensitive to be used for short exposures in large, oligotrophic Shield lakes. Conversion of oxygen-evolution to more conventional carbon-uptake values appears to be a questionable procedure in most Shield lakes, since there are marked diurnal variations in total CO_2, particularly in small lakes. Preliminary evidence indicates that low midsummer CO_2 concentrations are often limiting to primary production, and that they may be responsible for high PQ (photosynthetic quotient) values.

Most Shield waters were so low in electrolytes that normal glass-calomel electrode systems functioned erratically during *p*H measurements (Eisenman 1967). Again, the *p*H-change method was too insensitive for use in unproductive lakes.

Foremost among the problems encountered with the commonly used ^{14}C method was the difficulty of determining total CO_2 ($=CO_2 + H_2CO_3 + HCO_3^- + CO_3^=$) with sufficient accuracy. The usual acid titration method proved unsuitable due to the difficulty of measuring *p*H as mentioned above, to the low concentration of total CO_2 (20–500 mmoles/m^3), and to interference by dissolved humic compounds (D. Povoledo, personal communication). The gravimetric CO_2 technique sometimes recommended (see Goldman 1963) was too cumbersome and time consuming, requiring several liters of water per analysis from a Shield lake. The concentration of inorganic carbon by dialysis into NaOH solution before titration (Johnson and Michalski 1970) would require 3–4 liters of sample per analysis in more dilute ELA lakes. Small lakes that were thermally or chemically stratified, or both, often had great vertical variation in total CO_2 within the euphotic zone, so that several samples had to be analyzed on each date of incubation. The problem was solved by using a gas chromatographic system capable of giving quick, accurate, and sensitive (lower limit 2 ± 1 μmole/liter) results at low CO_2 concentrations. This system is still being improved by Dr D. Povoledo (personal communication), and a full description is anticipated at a later date. Because of this development, the ^{14}C technique was chosen for production measurements beginning in 1969. The high sensitivity of the method and the ease with which processing of samples can be mechanized make it convenient for extensive survey work in areas of low production.

Because of the extremely low concentrations of total CO_2 in Shield waters, little ^{14}C was needed per incubation. Indeed, inoculations of too much radiocarbon might even enrich the sample with CO_2 in some waters. One microcurie per 125-ml bottle per 4-hr exposure was adequate for almost all Shield lakes during the ice-free season.

Our tests have shown that small ampoules, even if prepared commercially, vary by several percent in their ^{14}C content. Inoculations using small individual ampoules also proved very time consuming. For this reason we prefer the Cornwall automatic refilling pipette recommended by Goldman (1963), which allows faster and more accurate inoculations. We used inoculations of 0.5 ml per bottle, with an activity of 2 μc/ml in summer, and 10 μc/ml for work under winter ice cover.[2] Large (20–25 ml) ampoules of prepared stock solution, each containing an adequate volume of solution for a single set of determinations, were used. Each ampoule was calibrated on the day it was used, as outlined below.

Schindler (1966) outlined methods for using liquid scintillation counting in primary production work using a dioxane-base fluor for radioassay of both stock ^{14}C and millipore filters. This fluor gives higher efficiencies and requires less preparation than the popular Bray's fluor (Bray 1960). The addition of ½ ml of NCS solubilizer, a strong base (Nuclear Chicago Corp.), to each vial effectively retains all $^{14}CO_2$ over long periods. Ordinary bases have strong chemical quenching properties and are unsuitable for the purpose. An Eppendorf automatic micropipette (Brinkman Instruments, Toronto) was used for taking fast accurate subsamples of stock solution for calibration. The recently developed channels-ratio or external-standard channels-ratio techniques, using a set of calibrated samples of known quenching properties, were used to determine counting efficiency. Counting efficiencies usually range from 60 to 75% with modern equipment, a 2× improvement on efficiencies possible in 1966 (Schindler 1966).

The bottle holder currently used for in situ incubations is shown in Fig. 1. This holder has proved much more convenient than others the authors have used. A set of 21 bottles can be inoculated with ^{14}C and lowered into the lake in less than 3 min by experienced persons using such holders. No loss of bottles from these holders has been experienced, even when used in 6-ft seas on Lake Winnipeg.

Incubations for 4 hr at midday (10:00 AM–2:00 PM, 11:00 AM–3:00 PM) were normally used. Dark boxes and bottles used were similar to those described by Goldman (1963). Corrections to full-day photosynthesis were made by multiplying 4-hr production values by the ratio $\frac{I_o, \text{daily}}{I_o, 4\ \text{hr}}$, where I_o is the surface solar radiation. Tests indicated that such extrapolations caused little error (Schindler 1971a).

Errors in filtration described by Arthur and Rigler (1967) appear to constitute one of the major sources of error in the ^{14}C technique (Schindler 1971a). This filtration error in our studies ranged from 1.2 to 6.1 times uncorrected filter activities in Shield lakes, and

[2]Winter production values are given by Schindler (1971a).

was larger in lakes dominated by nannoplankton. This effect was corrected by filtering and counting aliquots of several sizes from a well-mixed sample, then plotting the results and extrapolating the curve of dpm/ml vs. ml filtered to 0 ml (=0 thickness on filter). Figure 2 shows an example of such a plot constructed from a single sample from lake 132 at Kenora, using membrane filters of two pore sizes, 0.22 and 0.45 μ. The good agreement between the two plots is evidence for the validity of the technique. Such a series of filters gives a combined correction for filtration error and self-absorption when a planchet counter is used, so that the more commonly used but tedious and inaccurate $BaCO_3$ method is not necessary (see, for example, Strickland and Parsons 1968).

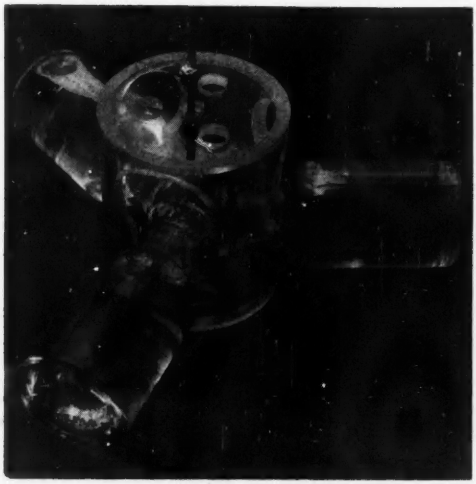

FIG. 1. A holder for incubation bottles used in in situ determinations of phytoplankton production.

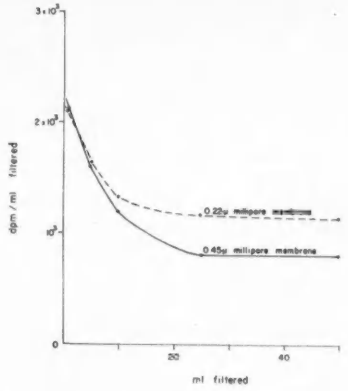

FIG. 2. An example of the correction curve for filtration error as applied to production results. The pore size of filters is given in the figure.

The same fluor discussed earlier (Schindler 1966) for determining the activity of stock ^{14}C solutions was used for assaying algae containing ^{14}C on membrane filters. Membranes were transferred from the filtration apparatus directly to vials filled with fluor. Loss of activity was negligible with this procedure, and samples could be stored indefinitely. Wallen and Geen (1968) have recently shown that filters stored in the usual dry state may suffer substantial losses of activity.

Several other fluors may be used to radioassay millipore filters by liquid scintillation counting. Of these the most commonly used is toluene (Lind and Campbell 1969; Wallen and Geen 1968; Pugh 1970). Although toluene fluors give extremely high counting efficiencies, they do not dissolve millipore filters completely, although the filters are cleared if they are dry when placed in the fluor. The addition of a small amount of dioxane to toluene fluors eliminates the need for drying filters with little reduction in counting efficiency. Toluene fluors have three other disadvantages: they are extremely flammable; since filters are not dissolved, self-absorption is high (Pugh 1970); and they pass through the walls of polyethylene scintillator vials, which are the most convenient type to carry in the field. NCS, the quaternary ammonium hydroxide mentioned above, will dissolve millipore filters (though not completely) if heated gently (<50 C). Since the resulting digest is dark colored, it must be bleached with strong peroxide or hypochlorite before addition of a toluene-base fluor for counting. Preparation is tedious and the base is expensive for routine use. Aquasol, a new xylene-base fluor that comes already prepared, dissolves millipore filters slowly, giving better counting efficiencies than dioxane-base fluors. It is also more costly.

If self-absorption by particles remaining undissolved in any of the above fluors is suspected, results may be tested by combusting samples in an oxygen atmosphere and trapping the liberated $^{14}CO_2$ in NCS, NaOH, monoethanolamine, hyamine hydroxide, or phenethylamine (Ragland 1966; Belisie et al. 1968).

Quantifying the extracellular organic products of photosynthesis was simplified by the use of liquid scintillation and the dioxane fluor described. Samples of filtrate were acidified to a *p*H of approximately 3 and bubbled for 30 min with a CO_2-free gas in order to drive off the remaining ^{14}C in inorganic CO_2 compounds, then aliquots of filtrate were added directly to the fluor in the scintillator vials. Up to 25% water in the fluor caused little or no reduction in counting efficiency. Results should, of course, be corrected for the filtration error mentioned earlier, without which extracellular values would be erroneously high (Schindler 1971a). Production of extracellular products during 4-hr incubations on Shield waters was usually insignificant relative to cell uptake (less than 1% of total light bottle fixation). In contrast, Nalewajko (1966) found high production of extracellular products when Lake Ontario phytoplankton was cultured at low CO_2 concentrations. Further testing is necessary to obtain conclusive results from a variety of situations.

PHYTOPLANKTON STANDING CROP

Aliquots for identification, enumeration, and determination of phytoplankton biomass were taken from all water samples used for production determinations. Samples were fixed with Lugol's solution and processed by the Utermöhl (1958) method as modified by Nauwerck (1963) and Pechlaner (1967). This method may give accurate estimates of total biomass and species composition if applied by an adequate taxonomist, since even small and delicate cells are well preserved. The taxonomic works of Huber-Pestalozzi (1938, 1941, 1942, 1950), Skuja (1948, 1956, 1964), and Prescott (1961) were used for identifying phytoplankton. An average of 500 organisms per sample were enumerated.

Chlorophyll samples were processed by Mr F. A. J. Armstrong. See Armstrong and Schindler (1971) for methods.

Results and Discussion

Figure 3 shows midsummer profiles for autotrophic phytoplankton production, chlorophyll *a*, total CO_2, and the division of phytoplankton biomass among major taxonomic groups for all lakes studied. More detailed seasonal data, including dark-bottle results, will be given in later publications.

Midsummer production values ranged from 0.02 to 2.12 g C/m³·day and from 0.179 to 1.103 g C/m²·day. Chlorophyll concentrations ranged from 0.4 to 44 mg/m³ and from 5 to 98 mg/m² in the euphotic zone. The corresponding ranges for live phytoplankton biomass were 120–5400 mg/m³ and 2100–13,400 mg/m².

Large (>50 ha) deep lakes (161, 305, 239) showed little variation in total CO_2 with depth or season (see Fig. 3). Smaller strongly stratified lakes (240, 304, 230, 99) showed more variation in CO_2 with depth and season, total CO_2 generally being lower in epilimnetic and higher in hypolimnetic waters during summer stratification. Small shallow lakes with no summer stratification, such as lake 303, were generally low in CO_2 throughout the water column in summer.

Table 1 shows the average percentage composition of cell biomass and major species for all lakes. With three exceptions, the phytoplankton of all lakes was dominated by Chrysophyceae in midsummer. About half the cell biomass in lake 230 was of the blue-greens *Merismopedia punctata* and *Anabaena flos-aquae*. Diatoms in lake 303 were slightly more abundant than Chrysophyceae, probably causing the extremely low silica values for that lake (as low as 15 µg Si/liter in late summer, F. A. J. Armstrong, personal communication). *Synedra acus* v. *angustissima* was the dominant species. Lake 99 was dominated by *Scenedesmus denticulatus*, although it was found only at the bottom of the euphotic zone. More detailed taxonomic and ecological information will be published at a later date. More detailed notes on individual groups are given below.

PHYTOPLANKTON

Bacteriophyta — Although this group does not belong to phytoplankton proper and was not considered in the counts, it made up such a large part of plankton in hypo- and metalimnetic regions (also in the epilimnion in a few instances), that it must be included here. The most common organism was *Sideroderma dubium* Skuja, which reached its maximum abundance in the lower part of metalimnion in many of the studied lakes. In the hypolimnion *Siderocapsa geminata* Skuja, *Leptothrix echinata* Beger., *L. pseudovacuolata* (Perfilj.) Dorff., and *Lamprocystis roseo-persicina* (KG.) Schröt. were the dominant bacteria encountered.

Cyanophyta — Blue-green algae were found in all lakes, but no water blooms were observed. In lake 230 *Merismopedia punctata* Meyen made up almost half the algal biomass, but in other lakes *Gomphosphaeria lacustris* Chod., *Coelosphaerium kuetzingianum* Naeg., *Rhabdoderma gorskii* Wol., *R. sigmoidae* Moore et Carter, *R. lineare* Schmidle et Lauterb., *A. flos-aquae* (Lyngb.) Bréb., *Chroococcus limneticus* Lemm., and *C. prescottii* Drouet et Daily were usually the most important species in the epilimnion. In the lower part of the metalimnion in lakes of class B (see below) large quantities of *Oscillatoria lauterbornii* Schmidle and *Spirulina laxa*[3] G.M. Smith were found together with *Sideroderma dubium*.

Chlorophyta — The green algae were usually rather insignificant quantitatively except in lake 99, where a large population of *S. denticulatus* Lagerh. occurred in the upper part of the thermocline. In the other lakes *Ankistrodesmus acicularis* A. Br., *Oocystis submarina variabilis* Skuja, *Pediastrum tetras* (Ehr.) Ralfs, *Elakatothrix gelatinosa* Wille, *Crucigenia tetrapedia* (Kirchn.) W. et G. S. West, *Gloeccoccus schroeteri* (Chod) Lemm., *Spondylosium* spp., and *Chlamydomonas* spp. were the dominant forms. The only important desmid was *Arthrodesmus incus* (Breb.) Hass., although a few *Staurastrum* spp. were occasionally found.

Euglenophyta — This group was the least important one in the ELA and only occasional *Phacus*

[3]Possibly *Lyngbya pseudospirulina* (Pascher) in some lakes, since a sheath was found in a few instances when live material was examined.

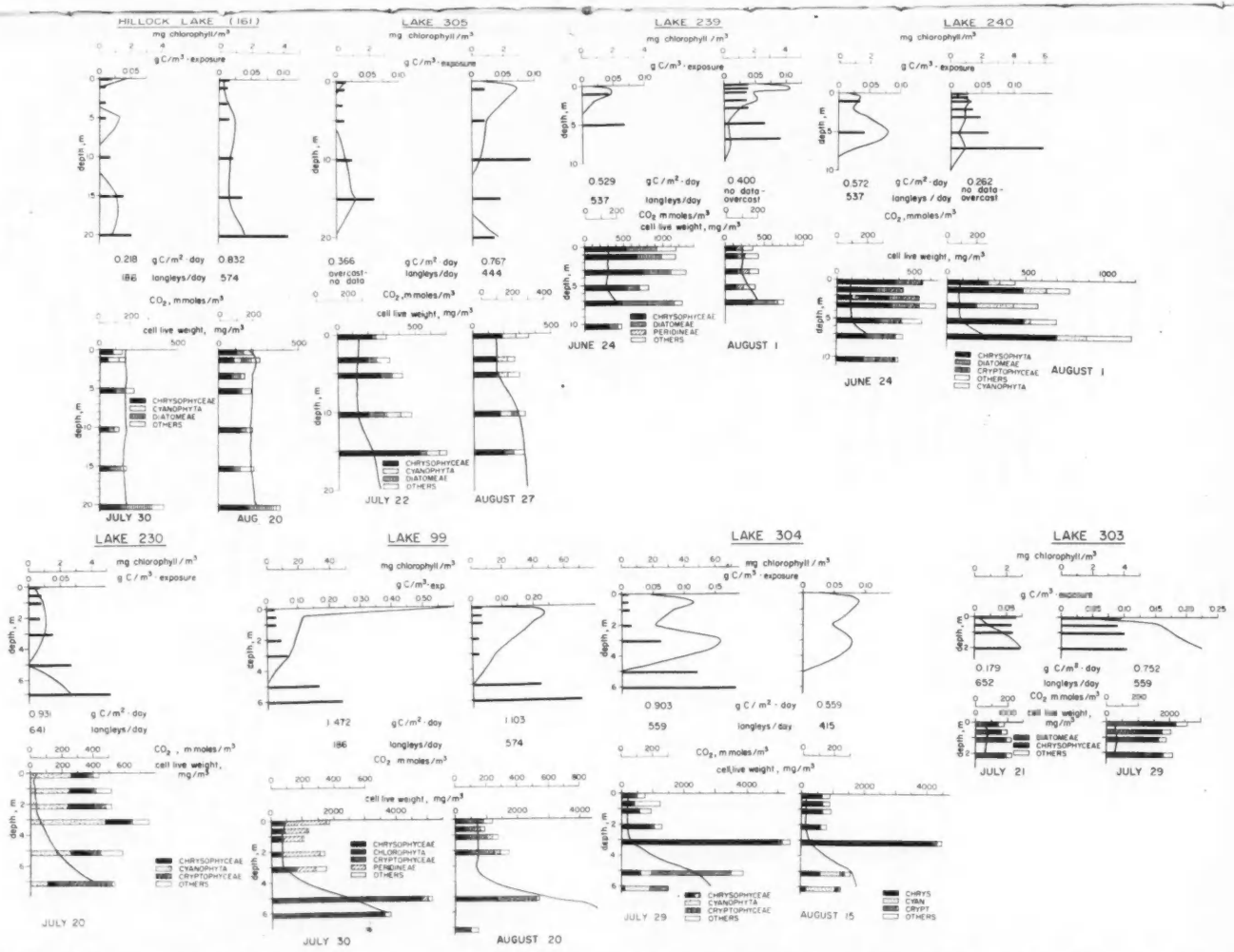

FIG. 3. Midsummer phytoplankton production, biomass, and chlorophyll *a*, total CO_2 and incident light from several ELA lakes. When possible 1 bright and 1 overcast day are shown for each lake. In the upper panels, the line and bars represent production and chlorophyll *a*, respectively; in the lower panels, CO_2 and phytoplankton biomass. Exposures were 10:00 AM–2:00 PM or 11:00 AM–3:00 PM. Primary production measurements were made at the depths of phytoplankton samples.

spp., *Lepocinclis* spp., *Euglena* spp., and *Peranema* spp. were found in the hypolimnion. In lake 240 a rather large *Euglena* population occurred in the epilimnion in late spring and early summer and *Trachelomonas* spp. were formed in small numbers in all lakes, both in hypo- and epilimnion.

Chrysophyta

Chrysophyceae — This was the largest algal group in ELA with the genera *Dinobryon*, *Mallomonas*, *Ochromonas*, and *Chromulina* most important. The species were *Dinobryon crenulatum* W. et G. S. West, *D. sertularia* var. *protuberans* (Lemm.) Krieger, *D. cylindricum* Imhof *s. str.* and var. *palustre* Lemm., *D. bavaricum* Imhof., *D. sociale* Ehr. *s. str.* and var. *americanum* (Brunnth.) Bachm., and *D. divergens* Imhof. The most common *Mallomonas* was an undescribed form, which probably is rather close to *M. pumilio* Harris et Bradley. *Mallomonas caudata* Iwanoff and *M. elongata* Rev. were also very common. Other important species were *Chrysosphaerella longispina* Lauterb., *Stichogloea doederleinii* (Schmidle) Wille, *Pseudokephyrion* spp., *Kephyrion* spp., and *Bitrichia longispina* (Lund) Bourr. The class Heterokontae (Xanthophyceae) has been included in the Chrysophyceae and was represented mainly by three species in the ELA: *Botryococcus braunii* Kütz., *B. protuberans* W. et G. S. West, and *Gloeobotrys limneticus* (G. M. Smith) Pascher. *Isthmochloron trispinatum* (W. et G. S. West) Skuja was occasionally found in most lakes.

Bacillariophyceae — The diatoms were important in lakes of class A and C, although they usually made up a very insignificant part of the biomass in lakes of class B (see below). *Synedra acus* v. *radians* (Kütz.) Hust., *S. acus* v. *angustissima* Grun., *Asterionella formosa* Hass., *Cyclotella*

Table 1. Phytoplankton and chlorophyll *a* in the euphotic zone of several ELA lakes (average values of counts from 0, 1, 2, 3, 5, 7, and 10 m), % abundance of algal groups. Underlining denotes importance of genera: solid line, >30% of total biomass; broken line, 5–30%; no underline, <5%.

Lake	Date (*1969*)	Cyanophyta	Chlorophyta	Chrysophyceae	Diatomeae	Cryptophyceae	Peridineae	Euglenophyta	Chlorophyll *a* (mg/m^3)	Live biomass (mg/m^3)	
161	July 30	7	10	39	34	1	10	0	0.9	244	*Chromulina, Botryococcus, Tabellaria*
161	Aug. 20	8	5	48	27	6	6	0	1.2	234	*Ochromonas, Rhizosolenia, Cyclotella*
305	July 22	9	3	62	14	6	5	0	0.9	448	*Ochromonas, Botryococcus, Chromulina*
305	Aug. 27	20	3	54	10	9	4	0	1.7	317	*Tabellaria, Dinobryon, Coelosphaerium, Cryptomonas*
239	June 24	2	3	53	31	7	4	0	1.7	1029	*Dinobryon, Rhizosolenia, Cryptomonas, Chromulina*
239	Aug. 1	2	5	40	18	17	19	0	1.9	462	*Synedra, Ochromonas, Botryococcus*
240	June 24	5	9	56	16	12	2	0	1.6	514	*Chrysosphaerella, Botryococcus, Dinobryon*
240	Aug. 1	18	2	58	7	8	7	0	2.4	733	*Cryptomonas, Cyclotella, Gloeobotrys, Mallomonas*
230	July 20	46	1	20	0	18	14	0	1.8	560	*Merismopedia, Cryptomonas, Gymnodinium, Botryococcus, Gloeobotrys, Dinobryon, Anabaena*
304	Sept. 29	10	4	54	1	24	5	2	10	2160	*Ochromonas, Cryptomonas, Dinobryon, Chromulina*
304	Aug. 15	14	5	69	1	8	3	1	–	1558	*Gymnodinium, Spirulina, Oscillatoria*
99	July 30	2	57	7	0	6	28	0	7.8	2725	*Scenedesmus, Gymnodinium, Cryptomonas, Synedra*
99	Aug. 20	2	30	15	21	23	9	0	5.8	1454	*Dinobryon, Chromulina*
303	July 21	2	9	32	48	4	6	0	2.6	1045	*Synedra, Dinobryon, Gymnodinium, Peridinium*
303	July 29	3	5	40	45	1	6	0	–	2167	*Cryptomonas, Arthrodesmus*

comta (Ehr.) Kütz., *C. stelligera* Cl. et Grun., *Tabellaria fenestrata* (Lyngb.) Kg., *T. flocculosa* (Roth) Kütz., *Rhizosolenia longiseta* Zach., and *R. eriensis* H. L. Smith were the most common species.

Pyrrophyta

Cryptophyceae — The cryptomonads were important in all lakes and were usually more numerous in the lower part of epilimnion or in the metalimnion. The taxonomy is difficult and many species are probably not yet described. The following have been identified: *Rhodomonas minuta* Skuja, *R. lacustris* Pascher et Ruttner, *Cryptomonas pusilla* Bachm., *C. ovata* Ehrnb., *C. obovata* Skuja, *C. marssonii* Skuja, *C. borealis* Skuja, *C. rostratiformes* Skuja, *Katablepharis ovalis* Skuja, and *Cryptaulax* spp.

Peridineae — The dinoflagellates were found in all lakes and usually formed an important part of the algal biomass, especially in lakes of class C. The most common species was *Peridinium inconspicuum* Lemm., which occurred in virtually all samples. Other species of this genus were *P. willei* Huitf-Kaas, *P. palustre* (Lindem.) Lef., *P. wisconsiense* Eddy, and *P. goslaviense* Wol. The genera *Gymnodinium* and *Glenodinium* were common, but the difficult taxonomy and many undescribed forms allowed few identifications. *Gymnodinium palustre* Shilling was found in most lakes and *G. helveticum* Penard occurred mainly in the metalimnion or hypolimnion. *Ceratium hirundinella* (O.F.M.) Schrank was found occasionally in most lakes, but seldom made up much of the biomass. Detailed lists of species in all lakes will be given in later publications.

Classification of ELA Lakes

A classification of lake types on the basis of phytoplankton production was attempted. The types of production–depth curves encountered in the ELA were strikingly similar to those described by Findenegg (1964). We have therefore used his classification as a basis for our own. The reasons given by Findenegg for the different types of production curves do not, however, apply in all instances. Some discussion is therefore devoted to this topic below.

Findenegg defined a class 1 lake as having a distinct production maximum in the upper epilimnion (but not at the very surface), followed by a rapid decline deeper in the water column. He described this type of curve as characteristic of "lakes rich in phytoplankton.... with low light penetration.... and all the other qualities characteristic of eutrophic lakes." Lakes 99, 239, and 240 exhibited the characteristic shape of production–depth curve for this class on most dates, but showed no other qualities associated with eutrophy, such as high phytoplankton standing crop, high nutrient concentrations (Armstrong and Schindler 1971), or high absolute values for phytoplankton production. It is likely that the key determining factor for this type of production curve is low light penetration, whether due to abundant phytoplankton as in eutrophic lakes, or to water color as in the three lakes mentioned above. The "other qualities" referred to by Findenegg probably play a relatively minor role in controlling the shape of the production–depth curve. Lake 303 is probably also of this type, although it is too shallow to exhibit the lower part of the characteristic curve.

Findenegg defined a class 2 lake as one having a production–depth curve without a distinct maximum. He believed that low rates of production were due to nutrient deficiencies, and that radiation was not a limiting factor within the euphotic zone. Although lake 161 is of this type and lake 305 is perhaps intermediate between class 1 and 2, it is difficult to prove that nutrients are more limiting in these lakes than in others of ELA, where levels of dissolved inorganic nitrogen, phosphorus, silica, and carbon are equally low. An investigation of availability of these nutrients is required before definite conclusions may be drawn. No lakes with colored waters would be expected in class 2.

Findenegg's class 3 is characterized by a dichotomic production–depth curve with a second production maximum during stagnation, usually occurring in the metalimnion of the lake. The European lakes exhibiting this type of curve are usually those recently exposed to cultural eutrophication. They typically display metalimnetic blooms of *Oscillatoria rubescens* (Ravera and Vollenweider 1968). The maximum rate of production per unit area is usually reached in this stage of lake succession. Further eutrophication, although accompanied by larger phytoplankton standing crops, results in reduced areal production because of decreased light penetration. None of the lakes in our study area have been exposed to cultural influences, yet the class 3 type of production–depth curve is very common. A more general explanation therefore seems plausible. ELA lakes exhibiting the characteristic production curve were always thermally stratified and rather shallow, with small hypolimnia that were anaerobic during most of the summer. All had hypolimnia that were rich in at least one nutrient relative to epilimnetic waters (Fig. 3; Armstrong and Schindler 1971,

and unpublished data) and all had euphotic zones extending well below the thermocline. The upper production maximum was probably due to optimum light conditions even though nutrients were relatively scarce; the lower maximum was the result of a more favorable nutrient regime (N, P, CO_2), which is an effective stimulant even at low light intensities. This type is undoubtedly characteristic of all lakes with a euphotic zone extending into a metalimnion or hypolimnion rich in nutrients. Both clear-water and brown-water lakes may be of this type, although in order to fulfill the required relation between thickness of epilimnion and light penetration a brown-water lake must be very small and protected. Lakes 230 and 304 shown here (Fig. 3) were of this class, as were 227, 122, and 81, mentioned in other sections of this publication. Schindler (1971a) discusses the matter further.

Findenegg's general observations on maximum midsummer production expected per unit area appear to be directly applicable to ELA lakes. Class 3 lakes usually had areal production at least as high as class 1. The mean maximum production for most ELA lakes was about 0.4 g $C/m^2 \cdot day$. Only very oligotrophic lakes (for example 161) and very shallow ones (for example 303) exhibited lower areal production values. A wider variety of areal production values is encountered when all Canadian Shield lakes are considered (Schindler 1971a). The extremely large lakes bordering the western edge of the Shield (Lake Winnipeg, Great Slave Lake, Great Bear Lake, and others) are all very unproductive, with production generally decreasing at higher latitudes. Slightly higher production is probably characteristic of lakes in the southern Canadian Shield of southeastern Ontario. Table 2 gives production values from a variety of lakes in Precambrian rock. The table probably embraces nearly the entire range of areas production values likely to be encountered in unpolluted lakes on the Canadian Shield.

In general, the average production per unit volume in the euphotic zone was very closely related to the live weight of phytoplankton (Fig. 4). This is not surprising in spite of the range of water colors, depths, and CO_2 concentrations encountered, since in more highly colored or shallower lakes, phytoplankton populations near the top of the water column are usually large.

The dominance of Chrysophyceae is a conspicuous feature of the ELA phytoplankton. The group contributes over 50% of the phytoplankton biomass in most lakes, at almost any season of the year. Although there are no published studies of the total biomass of phytoplankton in Canadian Shield lakes that are comprehensive enough to allow comparison, the data of Christie (1968) (based on ASPU units) also indicate that a predom-

TABLE 2. Typical midsummer primary production values from a variety of waters on the Precambrian Shield.

	N	W	Maximum production ($g\ C/m^3 \cdot day$)	Approximate maximum ($g\ C/m^2 \cdot day$)	Usual type of production curve
Eastern Great Bear L.	66°	120°	0.001	0.05	2
McLeod Bay, Great Slave L.	62	112	0.002	0.10	2
Eastern L. Winnipeg	52	98	0.030	0.05	1
Hillock L.	50	94	0.087	0.85	2
L. 305	50	94	0.142	0.85	1–2
Clear L.	45	79	0.260	2.57	1–2
L. 239	50	94	0.022	0.55	1
240	"		0.160	0.60	1
122	"		0.08	0.50	3
230	"		0.150	0.93	3
227	"		0.150	0.80	3
132	"		0.150	0.56	1
99	"		2.142	1.50	1
81	"		0.40	0.48	3
70	"		0.68	0.69	1
304	"		0.381	0.90	1–3
303	"		0.524	0.75	1
Coon L.	45	78	0.080	0.21	1
L. 241	50	94	0.046	0.130	Meromictic
120	50	94	0.020	0.100	Meromictic

inance of Chrysophyceae is likely to be a characteristic of Shield waters. Willén (1969) reports very similar assemblages for Precambrian areas of southern Sweden, although the average biomass of phytoplankton was somewhat lower in the lakes that he studied.

In the Kloten area in south-central Sweden, which is very similar geologically to ELA, the algal biomass and species composition are rather similar to ELA. A major difference is the small percentage of blue-greens and diatoms in the undisturbed Swedish lakes as compared with ELA (L. Ramberg, personal communication).

After even moderate disturbance by human activities the biomass of phytoplankton in Swedish lakes increased greatly and the species composition shifted to groups other than Chrysophyceae (Grönberg et al. 1968). Since none of the lakes studied here has been significantly disturbed to date, the dominance of Chrysophyceae is understandable, but the prominence of other groups in some lakes is somewhat puzzling when compared with the Swedish findings. An intercomparison of undisturbed lakes in terms of phytoplankton species composition on one or two dates alone is almost impossible as a result. Some rough guidelines may be set if one includes both phytoplankton biomass and species composition in the comparisons. The following scheme for typifying lakes is based on the classification by production mentioned earlier:

Class A

This includes lakes with both type 1 and 2 production–depth curves. In general, large or exposed lakes in the area are of this type, with most of the euphotic zone falling within the epilimnion. Live cell biomass seldom exceeds 1000 mg/m³. Combining with the production–depth classification would denote lake 161 as 2A, lakes 239 and 240 as 1A, and lake 305 as 1A–2A. Chrysophyceae usually dominate the phytoplankton throughout the euphotic zone. Major genera are given in Table 1.

Class B

This embraces small, deep, protected lakes, with the euphotic zone extending into a shallow, relatively rich hypolimnion. Cell biomass in the epilimnion is usually greater than 1000 mg/m³ and there are one or more pronounced cell maxima below the thermocline, with biomass exceeding that found in the epilimnion. The upper of the metalimnetic or hypolimnetic maxima usually consists of the chrysophytes *Dinobryon* spp. and *Ochromonas* spp. and the lower one (if present) of Cyanophyta (*Oscillatoria* spp. or *Spirulina* spp. *Lyngbya pseudospirulina*) or of *Cryptomonas* spp. Lakes 99, 230, and 304 are of this type. All of these were class 3 on the production scale above. Lakes 81, 227, and 122 have these characteristics.

A curious feature of this group of lakes is the high biomass of apparently healthy algal cells that lies deeper than the bottom of the euphotic zone as determined by ^{14}C measurements. Holmgren (1968) found that a similar metalimnetic maximum of *Cryptomonas* spp. in a lake of northern Sweden photosynthesized only on bright, completely cloudless days. Low temperatures and adequate nutrient supplies apparently allow such concentrations of phytoplankton either to maintain themselves or to

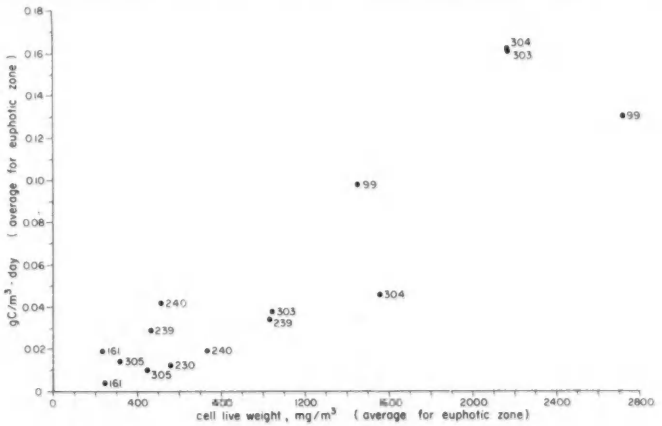

FIG. 4. Relation between production and live cell weight of phytoplankton in ELA lakes.

increase, even though adequate light may be limited to infrequent occasions. Heterotrophic CO_2 uptake does not appear to play an important role in maintaining such populations, since ^{14}C uptake in dark bottles is not unusually high.

Class C

This consists of shallow, weakly stratified lakes. Cell biomass over 1000 mg/m^3 is distributed uniformly throughout the water column. Diatoms (usually *Synedra acus* v. *angustissima*) were more important than Chrysophyceae in lake 303, which is of this class.

Some estimates of the time required for replacement of the algal population are possible, and of considerable interest since they give an idea of the activity of the phytoplankton population. Because no marked increases or decreases in phytoplankton biomass or production were observed in any lake immediately before or after the period studied (Holmgren and Schindler, unpublished data), the replacement time also serves as an index of how rapidly the phytoplankton biomass is passed on to higher trophic levels.

To convert all data to common units, phytoplankton biomass was converted to units of carbon, assuming that carbon supplies 10% of the live cell weight of phytoplankton (Strickland 1960). The total carbon content of the phytoplankton standing crop (g/m^2) in the euphotic zone is divided by the primary production in g C/m^2·day to obtain replacement time. Values so obtained ranged from 0.44 to 2.77 days, and appeared to be unrelated to light, nutrient, or lake type (Table 3). Several factors, including zooplankton grazing, are undoubtedly responsible.

Production per unit chlorophyll ranged from 0 to 23.4 mg C/mg chlorophyll *a*·hr. Highest values were found at the surface of lake 99 and at 1 m in lake 305. Euphotic zone averages ranged from 2.5 to 6.4 mg C/mg·chlorophyll *a*·hr, with lakes 305 and 240 showing the lowest and highest averages, respectively. These ranges are comparable with those found by other authors. Schindler and Nighswander (1970) review the subject.

In a recent paper Platt (1969) outlined a technique for calculating a coefficient for light-corrected photosynthesis, k_b, defined as the contribution of photosynthetic processes to the total optical attenuation coefficient of light. He found that a linear relation between k_b and chlorophyll at any depth explained most of the variance in k_b in the sea.

Since the necessary light data (Schindler 1971b) and chlorophyll *a* measurements were available for most of the lakes in this study, we examined the k_b–chlorophyll relation (Fig. 5). It is clear that little relation exists between k_b and chlorophyll when several lakes are compared, possibly because the reduction in transparency is largely due to water color rather than to phytoplankton standing crop.

To test the possible effect of other environmental factors on k_b, the relations were analyzed by multiple regression analysis. In the first analysis, k_b values for all lakes, depths, and dates were regressed on the variables temperature, cell volume, light, CO_2, and chlorophyll (see Schindler 1971b, for temperature and light data). Complete data

TABLE 3. Calculated turnover times for the phytoplankton of several Shield lakes, based upon ^{14}C uptake and cell biomass.

Lake	Date (*1969*)	Phytoplankton (*mg C/m²*)	Cuptake (*mg/m²·day*)	Turnover time (*days*)
161	July 30	375	218	1.77
161	Aug. 20	447	832	0.54
305	July 22	1014	366	2.77
305	Aug. 27	635	767	0.83
239	June 24	484	529	0.91
239	Aug. 1	370	400	0.92
240	June 24	424	572	0.74
240	Aug. 1	710	262	2.71
230	July 20	406	932	0.44
99	July 30	941	1472	0.64
99	Aug. 20	869	1103	0.79
304	July 29	1344	903	1.49
304	Aug. 15	1018	559	1.82
303	July 21	209	179	1.17
303	July 29	433	752	0.58

were not available in all instances, therefore only 42 replicates of each variable were used in the analysis. Temperature and cell volume proved to be the only independent variables of significance, explaining a small, but significant proportion of the variance in k_b ($R^2 = 0.26$, $F = 7.23$, with 2 and 40 df).

A second analysis was performed using even fewer replicates, but a larger number of variables. Complete nutrient data were available for 19 of the lakes for which k_b could be calculated (at depths of 1, 5, 10, 15, and 20 m) (Armstrong and Schindler 1971, and unpublished data). Inclusion of PO_4-P, NO_3-N, and dissolved Si from the same dates with the variables used in the first analysis gave an entirely different picture. Light, chlorophyll, and CO_2 proved to be the only variables of significance, explaining 61% of the variance in k_b ($F = 5.35$, 3 and 16 df).

This difference in the results of the two analyses is not altogether surprising since the latter analysis is biased more strongly in favor of deeper lakes and deeper samples within a lake, where chemical data were more often collected to correspond with production determinations. Two very elementary conclusions may be drawn: that contrary to Platt's findings in the sea, k_b is dependent largely upon factors other than chlorophyll concentration in ELA lakes, and that these factors are likely to vary in relative importance from lake to lake.

On the trophic scale of Winberg (1963), the most productive Shield waters would be classed as mesotrophic, seldom having midsummer ^{14}C production values exceeding 0.5 g C/m²·day, or chlorophyll in excess of 10 µg/liter in the euphotic zone. The most unproductive lakes in the Canadian Shield, with ^{14}C production less than 0.1 g/m²·day and chlorophyll less than 0.1 µg/liter would rank among the world's most unproductive lakes.

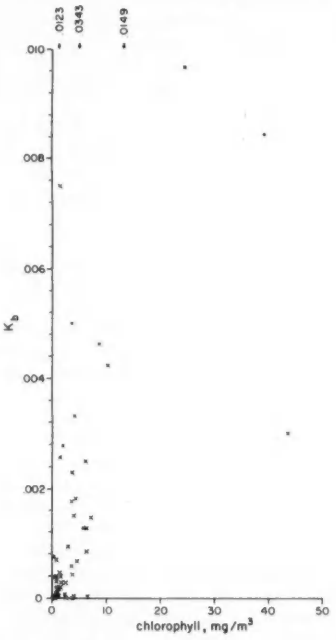

FIG. 5. Relation between k_b, the phytoplankton attenuation coefficient, and chlorophyll *a* concentration in several ELA lakes. All data are from midsummer experiments.

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R. Schmidt and H. Kling provided indispensable help with production measurements and phytoplankton counting. F. A. J. Armstrong supplied the chlorophyll *a* data. D. Povoledo assembled the gas chromatography apparatus used in this study. G. J. Brunskill provided valuable suggestions on techniques, and on the completed manuscript. J. Shearer and J. Johnson provided field assistance.

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Chemical Factors Involved in the Control of Phytoplankton Production in the Experimental Lakes Area, Northwestern Ontario[1]

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SAKAMOTO, M. 1971. Chemical factors involved in the control of phytoplankton production in the Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Bd. Canada 28: 203–213.

In short-term experiments (6 hr–3 days) the general order of decreasing importance of nutrients added individually to samples of lake water and contained phytoplankton was inorganic carbon, Fe, P, and N. The comparable order for long-term experiments (8–20 days) was P, Fe, N; or P, N, Fe. No relation was found between concentrations of chlorophyll and inorganic carbon in the lakes. The addition of iron and trace elements in chelated form and chelators (HEDTA, NTA) alone, increased photosynthetic carbon uptake. The deficiency of iron was mostly due to a lack of iron in a readily assimilable form.

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THIS study was undertaken to assess the relative importance of various nutrients in the control of phytoplankton production in the Fisheries Research Board Experimental Lakes Area (ELA), northwestern Ontario. Background limnological information on ELA is contained in other papers of this issue of the Journal of the Fisheries Research Board of Canada.

Three general approaches have been used to assess the importance of chemical factors for freshwater phytoplankton production: (1) observational data relating standing crops or photosynthetic production rates to chemical concentrations in natural waters (e.g., Lund 1949, 1950); (2) biochemical analysis of algae harvested from natural waters (Gerloff and Skoog 1957a, b; Fitzgerald and Nelson 1966; Fitzgerald 1969); and (3) changes in biomass or photosynthetic carbon uptake rates after enrichment with nutrients (e.g,. Thomas 1961; Goldman 1966; Wetzel 1966a, b).

The first two approaches do not require a modification of the natural environment, and for that reason yield valuable information on actual environmental situations. In spite of the fact that the third method is based on a change in the environment with the usual dangers of extrapolation from artificial conditions to processes operating within unmodified lakes, it offers the advantage that it is the only one in which the influence of various chemical factors can be studied both singly and in combination. With suitable caution it can yield valuable information that is difficult, if not impossible, to obtain by other means. This study was almost entirely based on enrichment tests.

Materials and Methods

The samples of lake water[3] used for the tests were either collected from just below the surface or as an integrated sample of the euphotic zone using the tube sampling method described by Armstrong and Schindler (1971). The samples were brought as rapidly as possible to the laboratory without warming, filtered through #30 bolting cloth to remove large zooplankters, and then mixed well and dispensed into transparent 125-ml Pyrex bottles or (occasionally) 250-ml Erlenmeyer flasks. After chemical enrichment, the samples were kept at low light intensity (approximately 100 ft-c) at a temperature close to, if not identical with that in the environment at the time of sampling. Samples collected during the summer of 1968 were kept in the above manner for 6 hr after chemical enrichment, and those collected after December 1968, for 24–72 hr after enrichment, prior to the first determination of photosynthetic carbon uptake. The times were varied to compensate for temperature differences.

Photosynthetic carbon uptake was determined by the addition of 0.5 ml of $Na^{14}CO_3$ solution (approximately

[1]The seventh in a series of 14 papers on the work of the Fisheries Research Board of Canada, describing background environmental data on the Experimental Lakes Area, northwestern Ontario. For location of numbered lakes see insert map at the back of this issue of the Journal of the Fisheries Research Board of Canada. A key to lake locations is given by Cleugh and Hauser (1971).

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[3]"Lake water" as used here should be interpreted to mean lake water with contained phytoplankton.

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2.5 μc) to duplicate samples from each flask, followed by incubation for 4 hr at the same temperature, under conditions of saturated light intensity (1500–2000 ft-c). A formalin solution containing Na_2EDTA (the disodium salt of ethylenediaminetetraacetic acid) was added at the end of the incubation period and the samples filtered through Millipore HA (0.45 μ) filters. Radioactivity was measured by liquid scintillation using Bray's fluor (Bray 1960). Most data are presented on a relative rather than absolute basis, i.e. in terms of counts per minute of radiocarbon retained by the filters in relation to controls. Results were considered significant only when treated samples differed from controls by at least 20%.

The form of the nutrients used was as follows: phosphates, nitrates, and bicarbonates as sodium salts; iron and trace elements as chlorides; and molybdenum as sodium molybdate. The concentrations of added N, P, and C were adjusted to lie within the usual range of concentrations observed in ELA lakes. The amounts of trace elements and vitamins added were arbitrarily selected on the basis of data from other lakes since the concentrations in ELA lakes were unknown.

A stock solution of each chemical was prepared with double distilled water before each experiment and added in 0–2 ml/bottle quantities to give the following concentrations of added nutrient: NaH_2PO_4, 0–20 μg P/liter, $NaNO_3$, 0–100 μg N/liter, inorganic C (as $NaHCO_3 + CO_2$), 0–7 mg C/liter. After adjusting the *p*H of the $NaHCO_3$ stock solution to 6.3 (close to the usual *p*H of most ELA surface waters) by bubbling with CO_2 gas, the solution used for injection was stored in a 50-ml syringe to prevent escape of CO_2 to the atmosphere. Approximately 50% of the C in the stock solution was in the form of $CO_2 + H_2CO_3$, and 50% as HCO_3^-. The total inorganic C content of the solution in the syringe was determined by absorption in $Ba(OH)_2$ and back titration with HCl. The iron + trace elements (Fe–Tr) solution was essentially as described by Provasoli (P.IV metals, Provasoli and Pintner 1960), but modified by dilution to one-fifth concentration and by the addition of $CuCl_2$. The amount added in various experiments ranged from 0 to 5 ml Fe–Tr solution per liter of lake water. Five ml of the Fe–Tr solution contained 40 μg Fe, 10 μg Mn, 5 μg Zn, 5 μg Mo, 1 μg Co, 0.2 μg Cu, and 1 mg HEDTA (N-hydroxyethylethylenediaminetriacetic acid). The concentrations of major cations and nutrients in the lakes at or near the time of sampling are given in Table 1.

The algae were identified by S. Holmgren and H. Kling. For details of nomenclature and authorities followed in the identification see Schindler and Holmgren (1971).

Results

Total CO_2

The terms "total CO_2" and "inorganic carbon" as used here refer to the sum of CO_2, H_2CO_3, HCO_3^-, and $CO_3^=$, expressed in terms of C. For all practical purposes $CO_3^=$ can be neglected in ELA surface waters because of the low *p*H range (5.4–7.5).

TABLE 1. Dissolved chemical constituents and chlorophyll *a* in surface waters from ELA lakes at or near my sampling dates. Data from F. A. J. Armstrong (unpublished) rounded to two significant figures. TDN = total dissolved N, TDP = total dissolved P.

		mg/liter					μg/liter					
Lake	Date	Ca	Mg	Na	K	Fe	NO_3-N	TDN	PO_4-P	TDP	Si	Chl. *a*
67	Oct. 22/68	1.6	0.8	0.8	0.25	0.03	<1	230	<1	10	110	2.2
69	"	2.2	1.1	0.9	0.38	0.01	17	200	1	6	160	14.0(?)
70	"	2.2	1.0	0.7	0.33	0.01	40	360	1	15	130	5.5
81	"	1.4	0.9	0.6	0.31	0.02	8	250	<1	8	150	4.4
82	"	5.6	1.0	1.0	0.45	0.01	39	440	<1	10	2300	4.9
122	Sept. 10/68	1.0	0.6	0.6	0.29	0.05	3	120	<1	6	50	1.5
132	Oct. 24/68	1.5	0.6	0.7	0.34	0.03	51	240	<1	10	92	1.8
149	Aug. 14/68	2.0	1.5	1.0	0.82	–	12	280	<1	14	670	2.5
150	Oct. 23/68	3.1	1.1	1.2	0.38	<0.01	30	380	<1	5	670	4.4
152	"	2.0	0.8	1.0	0.36	0.01	9	220	<1	19	380	1.9
253	"	2.3	0.8	0.9	0.40	0.01	10	260	<1	44	160	2.7
161	Nov. 14/68	2.4	0.7	0.7	0.31	0.01	28	290	2	8	130	1.3
239	Jan. 22/69	2.5	0.9	1.3	0.42	0.03	79	180	1	5	970	–
"	May 7/69	2.4	0.8	1.4	0.61	–	55	185	1	8	1700	1.8
"	June 5/69	2.2	0.8	1.2	0.50	–	24	143	3	24	750	2.7
"	Aug. 25/69	2.3	0.9	1.3	0.36	–	<1	135	2	11	2800	1.6
302	Oct. 22/68	1.7	0.6	0.6	0.30	–	5	130	<1	8	130	2.6
470[a]	May 7/69	1.2	0.6	0.9	0.35	–	7	140	<1	9	200	1.7

[a]Measured at the inflow to lake 240 (=outflow from lake 470).

Since total CO_2 concentrations in the surface waters of some ELA lakes were observed to be very low (e.g., 0.5–0.7 mg C/liter in the surface water of lake 122 in summer), the question arose as to whether total CO_2 might limit phytoplankton production in some lakes. Several experiments were undertaken to answer this question.

Figure 1A shows the relative increase in photosynthetic carbon uptake induced by the addition of $NaHCO_3$ (3.2 mg C/liter of lake water) to samples of water from several lakes. Note that this addition markedly stimulated carbon uptake in waters with a total CO_2 content less than 5 mg C/liter, and that the magnitude of the response was inversely proportional to the initial concentration of total CO_2.

The concentration of chlorophyll *a* in control samples (no enrichment with HCO_3^-) was also determined to compare the rates of photosynthetic carbon uptake on the basis of the amount of algae present. Figure 1B shows that the relative rates of photosynthetic carbon uptake per unit amount of chlorophyll *a* were proportional to the original concentrations of total CO_2 in the water samples.

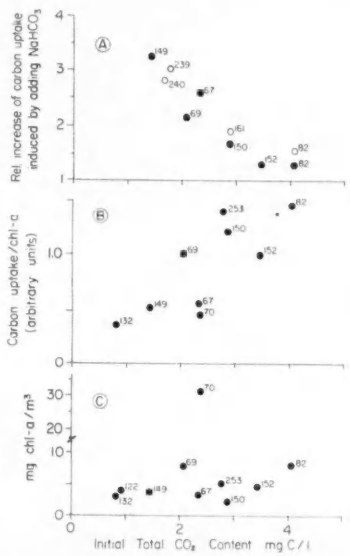
Rel. increase of carbon uptake induced by adding NaHCO3
Carbon uptake/chl-a (arbitrary units)
mg chl-a/m3
Initial Total CO2 Content mg C/l

FIG. 1. A, Relative photosynthetic carbon uptake values (enriched/control) after addition of $NaHCO_3$ (3.2 mg C/liter) vs. initial total CO_2 concentration in some ELA lake waters collected with a plastic tube in the euphotic zone in the summer of 1968 (●), and the surface waters in the winter of 1968–69 (○). B, Carbon uptake (arbitrary units) per unit chlorophyll *a* vs. total CO_2 concentration in some ELA lake waters in the summer of 1968. C, Chlorophyll *a* vs. total CO_2 concentration in ELA lake waters for the same samples as shown in A and B. The numbers refer to lake numbers (see insert map for location).

To determine whether a similar relation existed between total CO_2 and the biomass of phytoplankton in the actual lakes, a comparison was made between the average concentrations of total CO_2 and chlorophyll *a* in the euphotic zones of the lakes. The results are shown in Fig. 1C (see Table 2 for dates). No pronounced parallel was observed, indicating that although the addition of inorganic carbon stimulated photosynthetic carbon assimilation, no relation was found between inorganic carbon concentrations in the lakes and the biomass of phytoplankton.

Figure 2 shows the effects of adding increasing amounts of $KHCO_3$ and $NaHCO_3$ to samples of water from two ELA lakes in winter. The results, in conformity with those shown in Fig. 1A and B, indicate an enhancement of photosynthetic carbon uptake after the addition of $NaHCO_3$ and $KHCO_3$ for levels at least up to 5–7 mg C/liter.

On the basis of the above results it is concluded that concentrations of total CO_2 less than 5–7 mg C/liter limit photosynthetic carbon assimilation in ELA lake water samples as measured by short-term experiments, but no evidence was found of a comparable limitation in the lakes themselves in terms of biomass of algae and total CO_2.

Phosphorus, Nitrogen, and Trace Elements

Table 2 shows the relative increase in photosynthetic carbon uptake induced by the addition of phosphate, nitrate, and the Fe–Tr solution to samples of mixed euphotic zone water from several lakes in the summer of 1968. Significant positive effects were observed from the addition of the Fe–Tr solution to samples from lakes 67, 132, and 149; from the addition of phosphate to samples from lakes 67 and 69; from the addition of nitrate to samples from lakes 67 and 69; and from the addition of phosphate + nitrate to samples from lakes 67, 69, and 82. The addition of the Fe–Tr solution caused an equal or greater response than any other single additive in all lakes except lake 69, where addition of phosphorus induced the greatest response. It is also noteworthy that the addition of phosphorus and nitrogen, both alone and combined, to the samples of water from lakes 122 and 132 depressed photosynthetic carbon uptake.

In the above experiments, constant amounts of each chemical (30 μg NO_3-N/liter, 3 μg PO_4-P/liter,

5.0 ml of Fe–Tr/liter) were added to water samples. As is well known from the work of Rodhe (1948) and others, the optimum concentration of a given nutrient varies from species to species and also depends on the concentrations of other chemicals in the system. Inhibitory effects may even be observed, similar to the results shown in Table 2 for lakes 122 and 132. For these reasons all subsequent experiments were conducted using a variety of nutrients in different concentrations and combinations.

Figure 3 shows the effects of chemical additions on the rate of photosynthetic carbon uptake of water from lake 132 in December 1968. The only

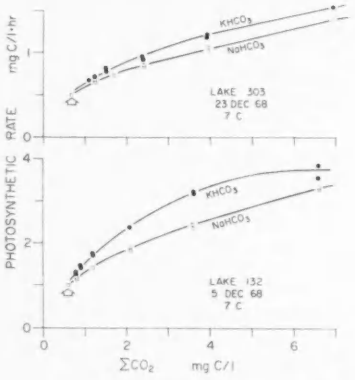

FIG. 2. Effects of enrichment with $NaHCO_3$ and $KHCO_3$ on photosynthetic carbon uptake of ELA surface waters. The abscissa is in units of the original plus added total CO_2. The arrows show the initial total CO_2 values of the samples.

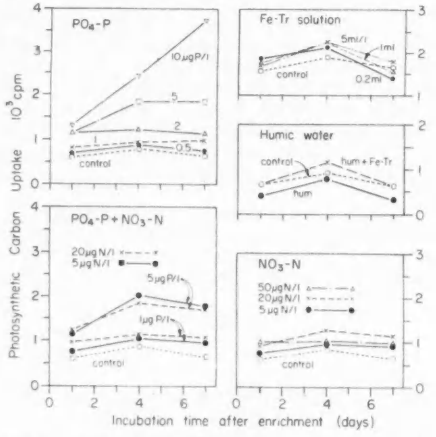

FIG. 3. Effects of added chemicals on photosynthetic carbon uptake of surface water samples from lake 132, Dec. 5, 1968. Incubation temperature, 7–10 C. Open circles show carbon uptake values of the control samples without enrichment.

TABLE 2. Relative photosynthetic carbon uptake for natural phytoplankton samples (1968) of several ELA lakes as measured by ^{14}C 6 hr after enrichment with nutrient salts. The plankton samples represent a mixed sample collected with a plastic tube in the euphotic zone. The amounts of nutrient chemicals added were 30 µg NO_3-N/liter, 3 µg PO_4-P/liter, 5 ml/liter of chelated Fe–Tr element solution, and 1 ml/liter of vitamin solution (thiamine HCl, 100 mg/liter vitamin B_{12}, 0.5 mg/liter. Concentrations are before enrichment.

Lake:	149	150	152	67	69	82	132[a]	122[b]
Date:	Aug. 14	Aug. 14	Aug. 14	Aug. 15	Aug. 15	Aug. 15	Sept. 9	Sept. 10
Control	100%	100%	100%	100%	100%	100%	100%	100%
PO_4	96	92	110	141	143	117	67	77
NO_3	99	91	99	121	127	104	92	78
PO_4+NO_3	99	96	110	147	130	118	42	77
Fe-Tr	169	118	119	217	115	119	140	83
Vitamins	–	–	–	–	–	–	124	99
Total CO_2 mg C/liter[c]	1.44	2.88	3.45	2.35	2.11	4.08	0.87	0.91
NO_3-N µg N/liter[d]	12	12	1	8	3	3	2	1
PO_4-P µg P/liter[d]	1	1	1	1	1	1	0.2	1.4
Fe mg/liter[d]	–	–	0.06	0.06	0.09	0.02	0.01	0.02
Chl. *a* µg/liter[d]	3.4	2.3	5.5	3.0	7.7	9.0	2.6	3.6

[a]Dominant algae: Small unidentified bluegreens, *Gomphosphaeria lacustris*, *Ochromonas* sp., *Merismopedia tenuissima*, *Oocystis submarina* var. *variabilis*.

[b]Dominant algae: *Chromulina* sp., *Ochromonas* sp., *Chroococcus dispersus*, *Oocystis submarina* var. *variabilis*, *Cryptomonas pusilla*.

[c]Determined by titration before enrichment of samples.

[d]Measured by F. A. J. Armstrong before enrichment of samples.

pronounced effect from a single addition was from phosphorus. Nitrate, both alone and in the presence of phosphate, failed to bring about any major response. These results show that at the time of sampling phosphate probably was a major growth-limiting factor. This situation in December contrasts with that observed in the same lake during September of the same year (Table 2), at which time single additions of the Fe–Tr solution and vitamins yielded the only significant positive responses. Figure 3 shows that the response to addition of the Fe–Tr solution was positive on the 1st and 4th days of the experiments, but on the 7th day only positive at the highest level added. Note also that humic-rich water taken from a nearby stream (10 ml river water added to 90 ml of lake water) reduced photosynthetic carbon uptake, and that this inhibition was relieved by addition of the Fe–Tr solution to the mixture. The reduction in carbon uptake was much greater than could be accounted for in terms of possible nutrient dilution caused by addition of the river water. This last result suggested that humic and other natural chelating substances might reduce the availability of Fe–Tr metals to algae in ELA lakes. I shall return to this question later in the paper.

Figure 4 shows the effects of different nutrient additions on the photosynthetic carbon uptake of a water sample collected from lake 302 in December 1968. Figure 4A shows the effects of addition of NO_3, NO_3 + Fe–Tr solution, and NO_3 + Fe–Tr solution + Ca + Mg at levels of phosphate enrichment ranging from 0 to 20 g PO_4-P/liter. Figure 4B shows comparable information for levels of nitrate enrichment ranging from 0 to 100 μg NO_3-N/liter. Note that 1.5 days after enrichment the samples to which nitrate and phosphate had been added, both alone and together, had lower rates of photosynthetic carbon uptake than the control (nothing added). The addition of the Fe–Tr solution (5 ml/liter), on the other hand, brought about a positive response in tests made after 1.5 days, both alone (Table 3) and with other nutrients (Fig. 4). These facts suggest that the photosynthetic carbon uptake of the original algal population was not limited by nitrogen or phosphorus, but was by one or more components of the Fe–Tr solution. The "long-term" effects (8 days) of the various nutrient additions on carbon uptake values were all positive except for low additions of phosphate alone (Fig. 4A). In all instances the addition of phosphate and nitrate together brought about a greater response than either alone, with further enhancement in the presence of the Fe–Tr solution. The pronounced differences between the assays made at 1 and 8 days were probably due to changes in the dominant species and algal biomass present in the flasks, the enrichment tending to favor species with high nutrient requirements. This was not, however, checked in detail.

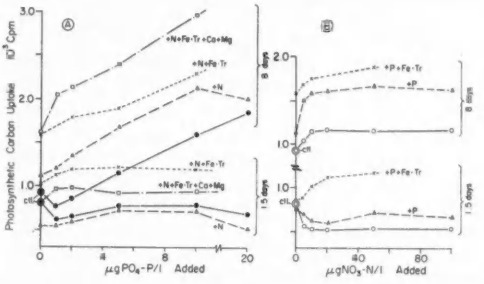

FIG. 4. Effects of chemical additions on photosynthetic carbon uptake of surface water samples from lake 302, December 1968, measured 1.5 and 8 days after incubation at 6–8 C. A, Effects of enrichment with N, N + Fe–Tr, and N + Fe–Tr + Ca + Mg at various levels of PO_4-P enrichment. B, Effects of enrichment with P, P + Fe–Tr, and P + Fe–Tr + Ca + Mg at various levels of NO_3-N enrichment. The amounts of added chemicals were: 50 μg NO_3-N/liter (A), 5 μg PO_4-P/liter (B), 5 ml Fe–Tr solution/liter, 2 mg Ca (as Cl salt)/liter, and 1 mg Mg (as Cl salt)/liter. Solid circles in A are for PO_4-P enrichment alone, and open circles in B for NO_3-N enrichment alone.

Figure 5 shows results of tests similar to those shown in Fig. 4 for lake 161 (Hillock) in January 1969. Although no decrease of photosynthetic carbon uptake was observed in assays made 2 days after the addition of nitrate alone, there was slight decrease from the addition of phosphate alone. The addition of the Fe–Tr solution alone (see Table 3) had no significant effect on carbon uptake at 2 or 10 days, but when added together with phosphate there was a significant stimulation. In most other respects the results from lake 161 resembled those from lake 302.

Figure 6 shows results obtained from lake 239 in January 1969, with assays made after 3 days of incubation. In general the results were similar to those obtained from lake 161, if the difference in incubation periods is taken into account. There was, however, a positive response from the addition of N alone to lake 161 water (Fig. 5) whereas this was not the case for lake 239. Note that the addition of the Fe–Tr solution alone (the point on the Fe–Tr curve in Fig. 6A corresponding to no addition of phosphate) failed to elicit a significant response, as was also the case for lake 161.

Table 3 shows the effect of various nutrient additions to water from three ELA lakes collected during the winter. In lake 81 (a brown-water lake)

TABLE 3. Relative photosynthetic carbon uptake of natural phytoplankton populations (0.5 m depth) of three ELA lakes. The amounts of added nutrients were as follows: 5 μg PO_4-P/liter, 50 μg NO_3-N/liter (except in lake 161 where it was 20 μg/liter), 2 mg Ca/liter, 1 mg Mg/liter, and Fe–Tr (iron and trace elements plus HEDTA) solution, 5 ml/liter.

Lake:	302		161		81[a]	
Date:	Dec. 1968		Jan. 1969		Dec. 1968	
Incubation temp (C):	6–8		4–5		6–8	
Days after enrichment:	1.5	8	2	10	1	10
Control	100%	100%	100%	100%	100%	100%
Ca+Mg	98	81	–	–	109	110
Fe–Tr	133	106	94	109	129	140
Fe–Tr+Ca+Mg	136	135	–	–	121	142
P	94	126	86	148	127	129
N	63	126	100	130	107	95
P+N	98	186	98	140	132	206
P+Fe–Tr	103	170	107	164	131	250
N+Fe–Tr	125	176	111	112	111	257
P+N+Fe–Tr	146	210	89	198	120	272
P+N+Fe–Tr+Ca+Mg	111	261	95	190	122	374

[a]Dominant algae at time of collection: *Katablepharis ovalis*, *Pseudokephyrion* spp., *Chromulina* sp., and *Dinobryon* spp.

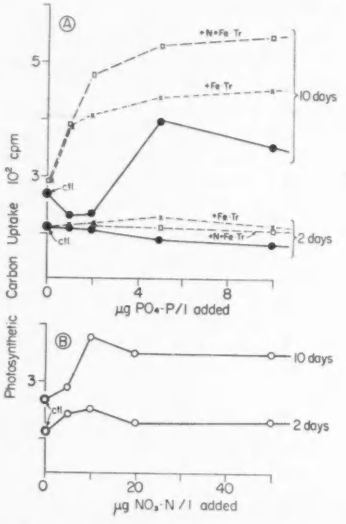

FIG. 5. Effects of chemical additions on photosynthetic carbon uptake of surface water samples from lake 161, January 1969, measured 2 and 10 days after incubation at 4–5 C. A, Effects of enrichment with Fe–Tr and N + Fe–Tr at various levels of PO_4-P enrichment. The concentrations added were 20 μg NO_3-N/liter and 5 ml Fe–Tr solution/liter. Solid circles are for PO_4-P enrichment alone. B, Effects of enrichment with NO_3-N. Dominant algae at the time of collection were *Ochromonas*, *Chromulina*, and *Katablepharis*.

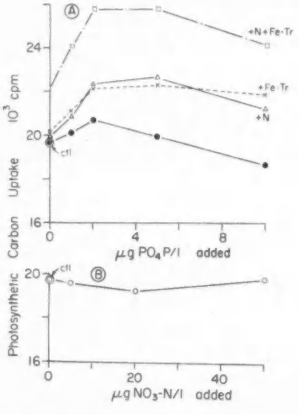

FIG. 6. Effects of chemical additions on photosynthetic carbon uptake of surface water samples from lake 239, January 1969, measured 3 days after incubation at 4–5 C. A, Effects of enrichment with N, Fe–Tr, and N + Fe–Tr at various levels of PO_4-P enrichment. The concentrations added were 20 μg NO_3-N/liter and 5 ml Fe–Tr solution/liter. Solid circles are for PO_4-P enrichment alone. B, Effects of enrichment with NO_3-N. Dominant algae at time of collection were *Chromulina* sp., *Rhodomonas minuta*, *Ochromonas* sp., and *Cryptomonas pusilla*.

the addition of phosphate alone and the Fe–Tr solution alone resulted in positive responses measured after 1 and 10 days of incubation. Significant responses were not observed from the addition of nitrate or Ca + Mg, when added alone. In most instances the addition of the Fe–Tr solution along with other nutrients resulted in significantly greater uptake after 8–10 days than for the same nutrients without Fe–Tr.

In interpreting the above results it is important to bear in mind that they pertain to artificial conditions in the laboratory. The concentrations of nutrients added ranged from zero to several times those present in the water at the time of sampling, i.e., not unrealistically high in terms of seasonal fluctuations. The "short-term" responses to nutrient additions measured after 1–2 days probably have more significance in terms of nutrient deficiencies at the time of sampling than do the results obtained after longer periods of time. In the one instance where the specific composition of the algal populations was determined throughout the incubation period (lake 239, May 1969, see Fig. 10) a definite succession of dominant forms from *Ochromonas* and *Chromulina* to *Synedra* and *Ankistrodesmus falcatus* was observed, particularly in the presence of high concentrations of phosphate. In this sense the long-term experiments (8–10 days) probably illustrate the overall reaction of the initial community to nutrient additions more than nutritional deficiencies at the time of sampling. It must also be added that carbon uptake values in long-term experiments are not only influenced by changes in species composition, but also by changes in biomass. In terms of eutrophication, both the short and long-term responses are, of course, significant — the former in estimating nutrient deficiencies at the time of sampling, and the latter approximating an overall community response.

With respect to inferred nutrient deficiencies at the times of sampling in the lakes studied, the general order of decreasing nutritional deficiency was total CO_2, one or more components of the Fe–Tr solution, and phosphorus. Nitrogen was inferred to be deficient in only a few lakes (67, 69, 161). Ca and Mg occurred in sufficient supply. As expected, the combined addition of various nutrients elicited a greater response than when single components were added alone.

Influence of Chelating Substances

The Fe–Tr solution used in the above experiments contained HEDTA as a chelator. The question arose as to whether the effects observed from the addition of the Fe–Tr solution were due to the iron and trace elements or to the chelating action of HEDTA itself.

Figure 7 shows the effects of addition of PO_4, PO_4 + HEDTA, and PO_4 + Fe–Tr (containing HEDTA) on the photosynthetic carbon uptake of water from lake 161 collected in January 1969. The addition of HEDTA (1 mg/liter) in the presence of 0–10 µg (added) PO_4-P/liter had no significant effect when measured after 2 days of incubation. A depressant effect was noted in measurements made after 10 days of incubation. On the other hand, the addition of the same concentration of HEDTA along with iron and trace elements (as in the Fe–Tr solution) had a markedly stimulating effect compared to samples enriched with phosphate alone or phosphate + HEDTA, both after 2 and 10 days. These results suggested that the significant component of the Fe–Tr mixture in the case of lake 161 was not HEDTA; however, the various factors of concentration and the proportion of free chelator to initial metal complex were not separated well enough in this experiment to permit any rigorous conclusions.

Figure 8 shows the results of a short-term experiment (assay after 3 days incubation at 10 C) using water from lakes 36 (highly colored with humic matter) and 239 (moderately colored with humic matter). In these instances the several components of the Fe–Tr solution were added both

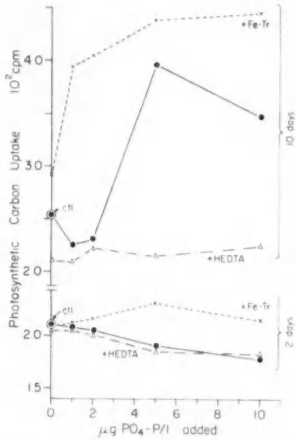

FIG. 7. Effects of chemical additions on photosynthetic carbon uptake of surface water samples from lake 161, January 1969, measured 2 and 10 days after incubation at 4–5 C for various levels of PO_4-P enrichment. Solid circles are for PO_4-P enrichment alone. Concentrations of chemicals added were HEDTA, 1 mg/liter; and Fe–Tr solution, 5 ml/liter.

individually and combined, and in the presence and absence of added phosphate + nitrate. The concentration of HEDTA used was 0.5 mg/liter. No significant effect was observed from any or all of the components in the case of lake 36 water. The response from lake 239 water was, however, significant when HEDTA, HEDTA + Fe, and HEDTA + Fe + trace elements were added. Except for Mn in the lake 239 samples enriched with N and P, no significant effects were observed from the addition of any trace element or vitamin.

In interpreting the response of lake 239 water to the addition of HEDTA-containing enrichments, the question arose as to whether the HEDTA used contained impurities that might account for the results. The HEDTA was found to contain 0.005% Fe. After checking the Fe content of several other chelators, nitrilotriacetate (NTA) and Na_3NTA were substituted for HEDTA in several later experiments. The samples used contained 0.003% Fe.

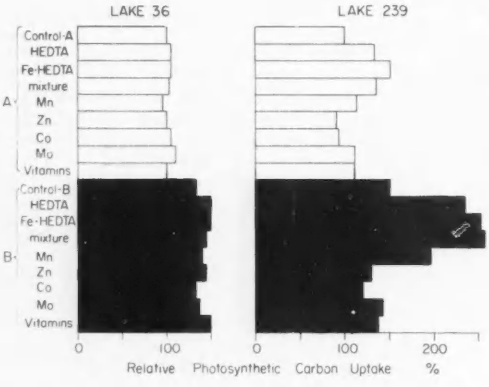

FIG. 8. Relative photosynthetic carbon uptake of surface water samples from lakes 36 and 239, August 1969, measured 3 days after incubation with added chemicals at 10 C: A, without added P + N; B, with 4 μg PO_4-P/liter and 20 μg NO_3-N/liter added in addition to the listed chemicals. The amount of each chemical added was: HEDTA, 0.5 mg/liter; $FeCl_3$, 20 μg Fe/liter; $MnCl_2$, 5 μg Mn/liter; $ZnCl_2$, 2.5 μg Zn/liter; $CoCl_2$, 0.5 μg Co/liter; $NaMoO_4$, 2.5 μg Mo/liter; vitamins, 100 μg thiamine HCl/liter, 0.5 μg vitamin B_{12}/liter. The mixture contained HEDTA, Fe, Mn, Zn, Co, and Mo in the above concentrations plus $CuCl_2$, 0.1 μg Cu/liter. The dominant algae at the time of sampling in lake 36 were *Chromulina* sp., *Erkenia subaequiciliata*, *Tetraëdron minimum*, *Cryptomonas pusilla*, and *Peridinium willei*; in lake 239, *Chrysococcus dispersus*, *Chrysosphaerella longispina*, *Chromulina* sp., *Merismopedia tenuissima*, *Tabellaria fenestrata*, and *Cryptomonas pusilla*.

Figure 9 shows the effect of adding $FeCl_3$ + trace elements, NTA, and $FeCl_3$ + trace elements + NTA on the photosynthetic carbon uptake of water from lake 470. Figure 10 shows the comparable effect of adding $FeCl_3$, NTA, and $FeCl_3$ + NTA to water from lake 239. In both instances (and also for data given in Fig. 10–12) the stock solutions of chelators were adjusted to *p*H 6.3 with

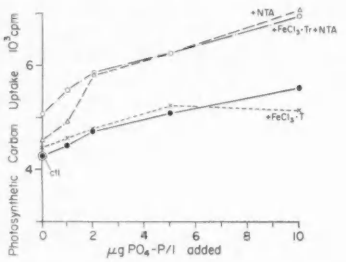

FIG. 9. Effects of chemical additions on photosynthetic carbon uptake of surface water samples from lake 470, May 1969, measured 3 days after incubation with added chemicals at 6–8 C with various levels of added PO_4-P. Solid circles are for PO_4-P addition alone. Concentrations of chemicals added were $FeCl_3$ + trace elements (62 μg Fe/liter, 40 μg Mn/liter, 10 μg Mo/liter, 5 μg Zn/liter, 1 μg Co/liter, 0.1 μg Cu/liter, *without chelator*) and NTA (500 mg/liter). The dominant algae at the time of sampling were *Chromulina* sp., *Pseudokephyrion* spp. *Katablepharis ovalis*, and *Ochromonas* sp.

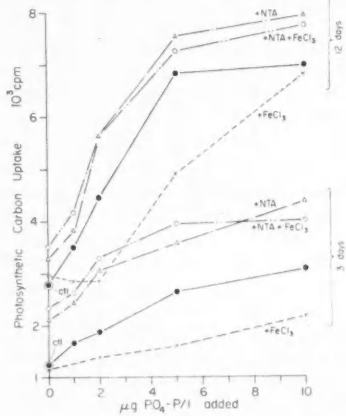

FIG. 10. Effects of addition of 500 μg NTA/liter and $FeCl_3$ (35 μg Fe/liter) alone and together on the photosynthetic carbon uptake of surface water samples from lake 239 (May 1969) 3 and 12 days after incubation at 6–8 C at various levels of added PO_4-P. Solid circles are for added PO_4-P alone.

NaOH. The experiments were conducted in the presence and absence of added phosphate (0–10 μg PO_4-P/liter). In both waters the addition of NTA with and without Fe enhanced photosynthetic carbon uptake to the same extent at all levels of added phosphate. The addition of $FeCl_3$ + trace elements to water from lake 470 resulted in no significant increase in photosynthetic carbon uptake at any level of added phosphate. The addition of $FeCl_3$ to water from lake 239, on the other hand, had a depressant effect in relation to controls with and without added phosphate. These results suggested that in lakes 239 and 470 the action of NTA was one of making iron or trace elements, or both, in their natural states more available to algae. This effect was the opposite of that observed from HEDTA addition to water from lake 161 in January (Fig. 7).

To compare the effects of different chelators, stock solutions of NTA, HEDTA, and citrate were added to water from lake 239 to yield concentrations ranging from 0.05 to 5.0 mg/liter. ^{14}C uptake was measured after 3 days of incubation. The similarity in the shapes of the curves for the three chelators (Fig. 11A) suggests that the stimulating effect on photosynthetic carbon uptake was due to the common chelating property of these compounds.

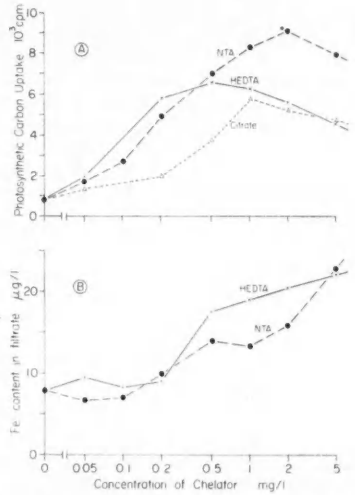

FIG. 11. A, Effects of three chelators on photosynthetic carbon uptake of surface water samples from lake 239 (June 1969), measured 3 days after incubation with added chelators at 10 C. B, Concentrations of total reactive iron in the filtrate after 3 days incubation with added chelators.

Many workers (e.g., Taylor 1964) have reported that chelating agents generally facilitate the utilization of iron and trace elements by algae in culture, yielding a greater growth than would otherwise be the case. It is apparent that this was also the case for ELA waters. At the *p*H prevailing in most ELA waters (5.4–7.5) iron and some trace elements could exist in particulate forms not readily available to algae. Figure 11B shows that the addition of NTA and HEDTA to unfiltered surface water from lake 239 did result in increased concentrations of iron in Millipore HA filtrates. There was also an approximate, though not exact, proportionality between the increase of iron in the filtrate and the magnitude of increase in photosynthetic carbon uptake (Fig. 11A).

Finally, Fig. 12 shows the results of an experiment using water from lake 239 to which nitrate, phosphate, NTA, and $FeCl_3$ were added in different combinations. There was no significant difference between the rates of carbon uptake for NTA and NTA + $FeCl_3$ in cultures with or without added nitrate and phosphate. The addition of $FeCl_3$ under the same conditions produced a lower carbon uptake during the first 8 days of culture, but thereafter the values approached those for NTA and NTA + $FeCl_3$. Cultures enriched with nitrate and phosphate were consistently lower than similar cultures with added NTA, and controls (no enrichment) were lowest of all. The results obtained

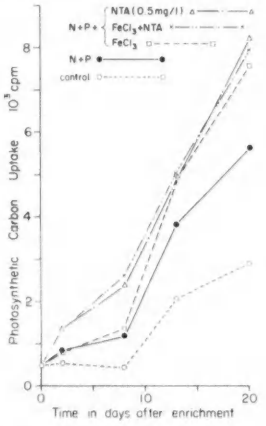

FIG. 12. Effects of chemical additions on photosynthetic carbon uptake of surface water samples from lake 239 (May 1969) incubated at 10 C and 200 ft-c of fluorescent light. The amounts of added chemicals were: $NaNO_3$ (50 μg N/liter), NaH_2PO_4 (5 μg P/liter), $FeCl_3$ (20 μg Fe/liter), NTA (0.5 mg/liter). Cultures were shaken by hand once a day.

at 2 days suggest that the original population was probably limited by N, P, and available Fe.

Discussion

The evidence presented in Fig. 1 and 2 suggests that total CO_2 (=inorganic-C) in the surface waters of ELA lakes probably limits algal growth at levels below 5–7 mg C/liter. This was earlier reported for other lakes on the Canadian Shield by Johnson et al. (1968) and Christie (1968). It is tempting to speculate from these findings that total CO_2 limitation may be a phenomenon of general significance in Shield waters. On the other hand there was no evidence that total CO_2 levels determined the biomass of phytoplankton in ELA lakes. Other factors were evidently involved in the lakes themselves.

In the above connection, reference must be made to the recent paper of Kuentzel (1969) that purports to show that carbon dioxide (as a molecule) is a major factor limiting the growth of algae in nature. Kuentzel, however, failed to realize that the molecular CO_2 is generated from bicarbonate as it is used, rather than from air, and that many algae grow at high *p*H values, i.e., under conditions of low CO_2 concentration. His arguments also pertain to populations of algae denser than those characteristic of ELA lakes and in any case have been criticized on other grounds by Shapiro (1970.) The growth-limiting effect of total CO_2 reported here should therefore not be confused with some of the growth-limiting effects claimed by Kuentzel.

Among other nutrients added singly, phosphorus was generally found to stimulate photosynthetic carbon uptake in long-term experiments, with nitrogen less effective in both the short- and long-term senses. In some instances the short-term effects of phosphorus and nitrogen additions were inhibitory; but the long-term response from combined phosphorus + nitrogen additions both in the work reported here and that of Armstrong et al. (unpublished data) was strongly positive.

As shown in Fig. 8, 9, 10, and 12 the addition of chelators alone caused a response similar to that brought about by chelated Fe, suggesting the importance of available iron rather than total iron as a factor limiting algal growth. A number of workers have examined problems of iron availability in natural waters. Rodhe (1948) found a parallel between the iron available to *Scenedesmus* for growth and iron as measured by reaction with *o*-phenanthroline, both accounting for only part of the total iron present in waters from lakes Erken and Siggeforasjön. Shapiro (1969a, b) likewise found that only a fraction of the total iron present in Minnesota lake waters was available for algal growth, but he was unable to confirm the parallel between availability to algae and reaction with *o*-phenanthroline that Rodhe had found. Other workers have studied the effects of adding chelators or chelated iron and trace elements to natural waters. Schelske (1962) and Schelske et al. (1962) found that the addition of chelated iron to a marl lake in Michigan brought about a marked increase in photosynthetic carbon uptake. From these results Schelske (1962) concluded that the availability of iron was a factor that limited primary production. Wetzel (1966a, b) likewise reported that chelated iron and manganese and also EDTA alone increased photosynthetic carbon uptake in waters of a marl lake in Indiana. Wetzel (1966a) attributed the EDTA effect to an increase in the availability of iron or other essential elements for algal growth.

In terms of natural chelating agents, Fogg and Westlake (1955) noted that the extracellular polypeptides produced by blue-green algae have chelation properties, and in the present work it has been found that the inhibitory action on carbon uptake observed from the addition of humic-rich stream water to water of lake 132 could be relieved by the addition of an Fe–Tr mixture. All these facts suggest the importance of natural chelating agents in relation to the availability of iron and trace elements, in some instances (EDTA, NTA) increasing the availability, in other instances (humic materials) apparently reducing the availability. In this connection it may be of paramount importance in future studies on ELA waters to examine more closely than I have done the relation between humic content and algal production in terms of the availability of iron and trace elements.

On the basis of the results reported here, it is difficult to make any exact statements about the relative importance of phosphorus, nitrogen, iron, and inorganic carbon in ELA waters. First of all, variations were encountered in the response to single and combined enrichments, both from lake to lake and time to time. Secondly, the addition of one nutrient or a combination of two or more nutrients can be expected to affect the relative order of nutritional importance of other nutrients. Also, the time required for a measurable response varies depending on the nutrient added.

On top of this, the physiological significance of a deficiency of iron or a trace element is quite different from a deficiency of carbon, nitrogen, or phosphorus, in that the last three serve as major structural components of cells. Best estimates of the decreasing order of importance of nutrients that

limit production in ELA waters are (with the above limitations): (1) short-term experiments (6 hr–3 days): total CO_2, Fe, P, N; (2) long-term experiments (8–20 days): P, Fe, N; or P, N, Fe.

The long-term effects of C addition have been studied separately (Schindler et al. unpublished data). Preliminary evidence suggests a lesser long-term role for C than for P, Fe, and N.

Acknowledgments

I am indebted to all the staff of the Eutrophication Section of the Freshwater Institute for advice and assistance in carrying out these studies, but especially to Dr J. R. Vallentyne for help in transforming my English into readable form, and to S. Holmgren and H. Kling for phytoplankton identification. This work was completed during a 2-year leave-of-absence from Nagoya University, Japan.

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Periphyton of the Experimental Lakes Area, Northwestern Ontario[1]

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The periphyton of four Experimental Lakes Area (ELA) lakes was examined in 1969. The littoral zone of all lakes was composed chiefly of large boulders and rock shelfs and the epilithic algal assemblage was accordingly dominant. Depending directly on light penetration and substrate availability benthic algal growth in most lakes was negligible at depths greater than 10 m. Throughout the growing season diatoms were the dominant algal group within the epilithic assemblage, comprising more than 60–70% of the total algal volume. Filamentous green and blue-green algae increased in importance in July and August but never constituted more than 40% of the volume of the total algal biomass. A well-defined diatom succession was observed both on the natural lithic substrate and on glass slides. *Achnanthes minutissima* was the most abundant diatom encountered in the littoral zone of all lakes. Periphyton growth on glass slides in lake 240 was 27 mg organic matter/m^2·day during initial colonization and 250 mg organic matter/m^2·day during the period of maximum growth. The vertical distribution of littoral diatoms in lake 240 was examined and differences among species are discussed in light of possible regulating mechanisms. *Achnanthes flexèlla* and *Eunotia pectinalis* were found only in the psammonal habitat of lake 240.

Statistical treatment of chemical analyses of N, P, and chlorophyll *a* content of periphyton showed no significant difference in amounts of total N among periphyton from lakes, but the distribution of both total P and chlorophyll *a* was significantly different among lakes examined. Highest concentrations of both P and chlorophyll *a* were found in lakes 239 and 227. In lake 227, a lake receiving weekly additions of N and P, concentrations of P were significantly greater than in the other lakes. Concentrations of N and P/unit organic weight of periphyton taken at a depth of 1 m in each of the study lakes were greatest in lake 227. Comparisons among lakes are made and, based on the results of these comparisons, the role of N and P as regulators of periphyton growth in the ELA lakes is discussed.

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LITTORAL algae play a substantial role in the energy cycle of Precambrian Shield lakes. The nutrient-poor water of these lakes does not support high limnetic production and the biomass of plankton populations is generally low (see Schindler and Holmgren 1971). The nature and abundance of available substrates, together with gradually sloping shorelines and relatively good light penetration, create what can be considered optimal conditions for littoral algal growth and production.

With only a single season's data it is too early to draw any definitive conclusions about the periphyton[2] communities of Experimental Lake Area (ELA) lakes. The intention of this communication is to describe the littoral habitats of four representative Shield lakes in ELA, discussing their similarities and differences with respect to the chemical and biological parameters measured to date. Results of more intensive studies of the littoral diatom community on both natural lithic substrates and on glass slides in lake 240 are compared with similar investigations by others on lakes at temperate latitudes. Results of this initial periphyton survey should provide meaningful direction for future

[1]The eighth in a series of 14 papers on the work of the Fisheries Research Board of Canada, describing background environmental data on the Experimental Lakes Area, northwestern Ontario. For location of numbered lakes see insert map at the back of this issue of the Journal of the Fisheries Research Board of Canada. A key to lake locations is given by Cleugh and Hauser (1971).

[2]The word "periphyton" as used throughout the text refers only to epilithophyton algae growing upon the surface of rocks. Some authors interpret periphyton in its broadest sense to include the faunal components. For a detailed discussion of the nomenclature of attached organisms in lakes see Wetzel (1964).

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studies of in situ periphyton algal production as well as baseline data for future studies of the response of littoral algae to artificial enrichment.

Description of Study Area

Studies of littoral algal communities commenced in April 1969. Four ELA lakes were chosen for intensive study: lake 305, a clear, deep oligotrophic lake; lake 227, a small sheltered lake selected for the 1969 lake fertilization experiment that commenced in June 1969; lakes 239 and 240, near the field station, good examples of slightly colored lakes with moderate depth (for further morphometric description see Brunskill and Schindler 1971). Most ELA lakes have boulder-strewn shorelines with some bedrock intrusions and widely scattered sandy beaches. Preliminary rough surveys of the littoral zones of two of the study lakes, 239 and 240 (see littoral maps, Fig. 1 and 2) showed approximately 70–80% of the littoral zone to a depth of 4 m to be composed of broken rock shelf, large boulders (50–100 cm diam), and coarse gravel (3–10 cm diam). About 15% was composed of sand and remaining portions consisted chiefly of organic sediment (silt and clay size) with widely scattered small rocks (10–30 cm diam). Shoreline slope in most ELA lakes was gradual, 5–10°, with an occasional, almost vertical, rock shelf, dropping off to depths greater than 5 m. There was sufficient light penetration (see Schindler 1971) to allow periphyton algal growth in excess of 10 m in lake 305, but in lakes 239 and 240, 5–6 m was the maximum depth of detectable growth. In lake 227 algal growth was restricted to the top 2.5–3.0 m for most of the summer. Water temperatures in the littoral zone were similar to those recorded for the epilimnion in these lakes (Schindler 1971), varying from a low of 4 C after ice left the lake to a high of 23 C in late August and early September. All substrates examined, with the exception of sand, had a furlike, light-brown growth of periphyton that varied seasonally in thickness from 0.5 to 2 cm. Rooted aquatic macrophytes were encountered in the littoral zone of most ELA lakes, and were most common in very shallow, gently sloping bays where organic sediment had accumulated.

Methods

Twelve trips were made to the study lakes between April 22 and November 23, 1969. In most instances, duplicate samples were obtained from the "splash zone"

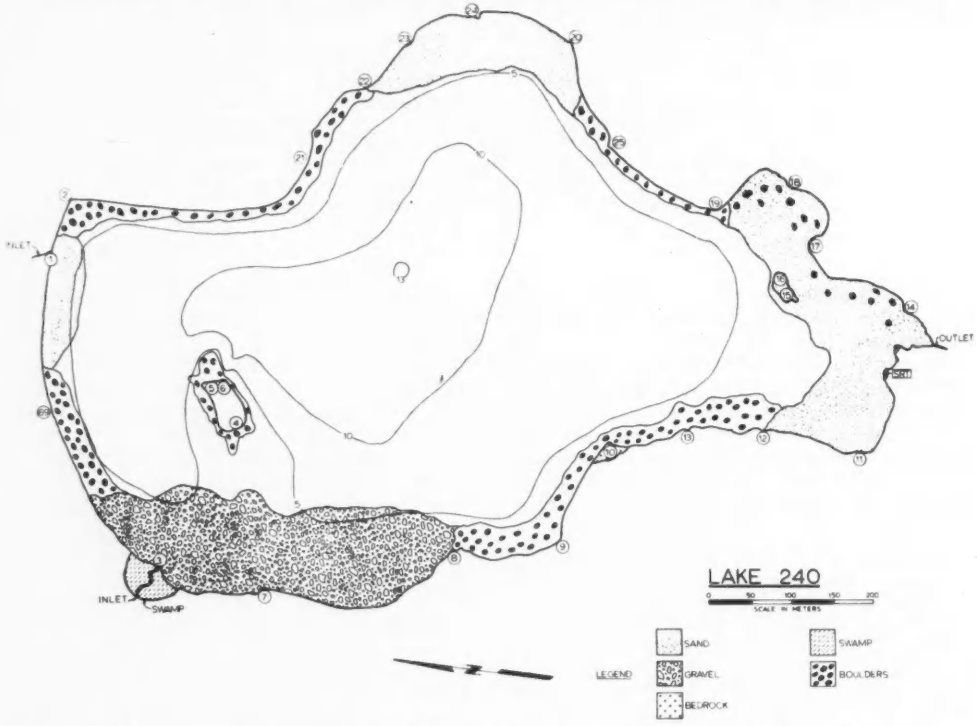

FIG. 1. Preliminary survey of the substratum in the littoral zone of lake 240. Numbers are bathymetric survey station locations (Brunskill and Schindler 1971).

(0–20 cm) and at 1-m intervals to a maximum depth of 5 m. By free-diving with mask and snorkle, samples were obtained at 3, 4, and 5 m. Rocks ranging in diameter from 10 to 20 cm were quantitatively sampled with a stiff nylon brush (toothbrush) attached with waterproof glue to the piston of a 50-cc disposable plastic syringe (Fig. 3). The sampler was placed firmly against the rock surface and the piston with brush tip rotated several times. The piston was slowly drawn up the barrel of the syringe, drawing the loose periphyton into the syringe. A glass plate was then placed over the end of the syringe and the sampler inverted. Examination of the scraped rock surface showed a satisfactory removal of all attached material from the rock, and there was no discernable damage to the algal cells in the process of removal. This apparatus scraped clean an area equal to 5.7 cm². Two scrapes were taken from each rock and placed in a 100-cc wide-mouthed jar. Replicate samples from a single rock shelf or large boulder were similar (20% variation between replicates), but the variation between small rocks at any given depth was much greater (35–40%). Samples so obtained were divided into three equal fractions for analysis: (1) chlorophyll *a*; (2) accumulated biomass (here defined as periphyton/unit area) for total C, N, and P; and (3) algal cell counts. Samples were filtered on Whatman GF/C glass fiber filter paper of 4.25 cm diam, and dried over silica gel. Both biomass and chlorophyll samples were frozen until analyzed, usually within a week of collection. All results were converted to a unit area basis after analysis. The following analytical procedures were used.

Chlorophyll

Two extraction procedures were used. Up to August 15 samples were extracted with about 6 cc of 90% acetone for 20–24 hr, in stoppered test tubes at 5 C in a refrigerator. The extracts were then filtered on Whatman GF/C filters in an all-glass apparatus, the original filter, the tube, and filter apparatus washed with small

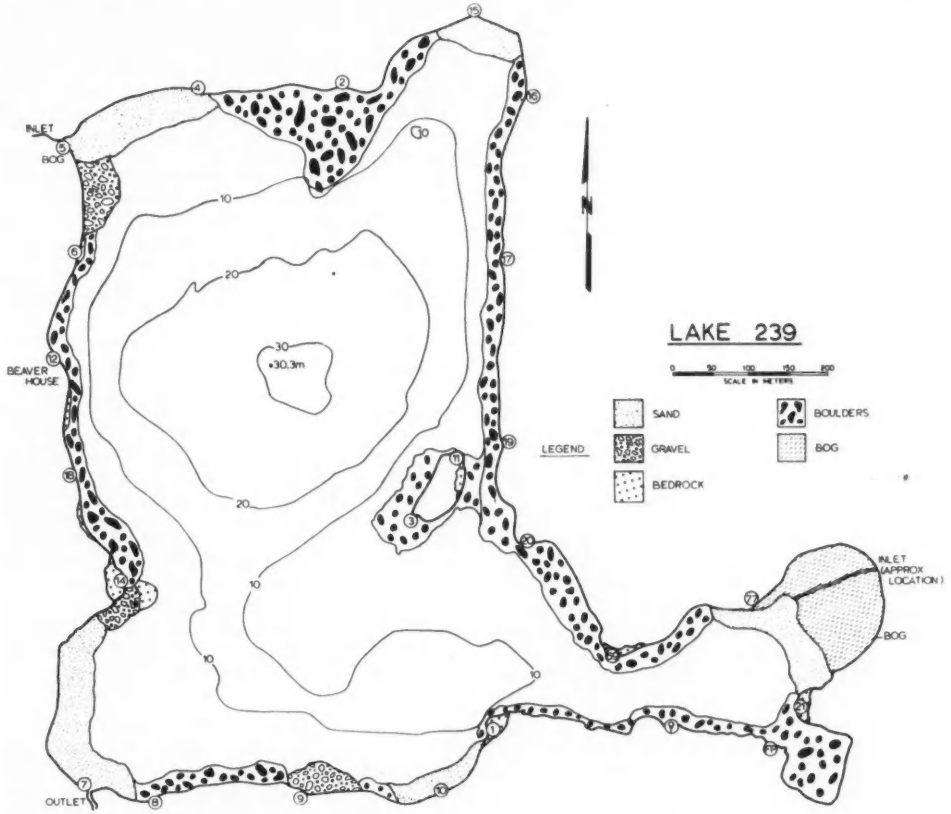

FIG. 2. A preliminary survey of the substratum of the littoral zone of lake 239. Numbers are bathymetric survey station locations (Brunskill and Schindler 1971).

portions of 90% acetone, and the volume of the filtrate adjusted to 10.0 cc. This filtration of the extracts gives less turbidity than centrifugation. By August there was much more organic material, often very dark in color, in the preparations, and we suspected that the extraction was incomplete. Some tests showed that appreciably more chlorophyll could be extracted if the sample was finely ground, and the procedure of Yentsch and Menzel (1963), using a tissue grinder, was used from August 28 onward.

Chlorophylls were determined spectrophotometrically by measurements at 750, 665, 645, and 630 nm, using the equations of Parsons and Strickland (1963). Chlorophyll *a* only is reported.

Organic Matter

The filter disc was handled only with forceps to avoid organic contamination, and was cut along a diameter to give equal halves of the collected material. Carbon and nitrogen were determined on one half and phosphorus on the other.

Carbon and Nitrogen

A Perkin-Elmer Model 240 Elemental Analyzer was used. This instrument has a Dumas-type combustion system, using helium and oxygen. Carbon dioxide, water, and molecular nitrogen are produced from organic material. C, H, and N are determined by differential thermal conductivity measurements of gas mixtures before and after absorption of CO_2 and H_2O, and by comparison with the helium supply. It is designed for analysis of all types of organic compounds, including refractory ones, and a combustion-tube temperature of 950 C is recommended. For our analyses the half-filter was rolled up and put into a silica ladle for insertion into the combustion zone, and 950 C was too high, since the glass of the filter fused to the silica. This caused destruction of the ladle in a few treatments. We have found that for these periphyton samples, combustion and oxidation are complete at 700 ± 20 C. At this temperature the borosilicate glass of the filter sinters without sticking to the ladle. A few tests showed that satisfactory recovery of carbon and nitrogen could also be obtained from benzoic acid, acetanilide, 3-5-dinitrobenzoic acid, chloramine T, and glycine.

The filters were ignited at 500 ± 20 C for 24 hr before being used to remove organic contamination; nevertheless blanks were appreciable. The carbon blank amounted to 5–10% of the carbon in the samples; it appeared to come from atmospheric CO_2 held on the filter, since the instrument blank was usually too small to measure. On the other hand, the nitrogen blank, which was relatively larger, amounting to 10–20% of the nitrogen in the sample, was mostly instrumental, possibly from the helium supply remaining rather constant. The part from the filters was only just measurable.

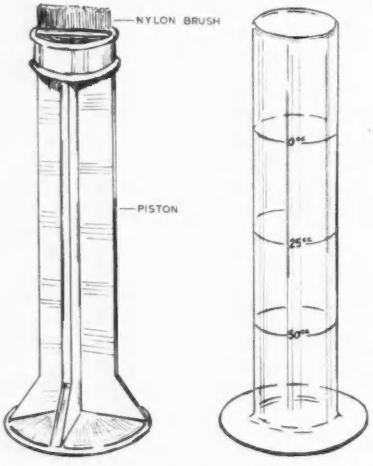

Fig. 3. Periphyton sampler made from a disposable plastic syringe and used in this study. Brush is cut from a nylon toothbrush.

Phosphorus

The half-filter disc for this determination was placed in a 50-cc borosilicate beaker and ignited in a furnace at 500 ± 20 C to destroy organic matter. This low temperature avoids volatilization of phosphorus (see below) and fusion of the residue and glass filter paper. The residue was boiled with 10 cc of 0.2 N HCl to dissolve and hydrolyze ortho-phosphates and any condensed phosphates that had been produced by the ignition. The solution was filtered, diluted to 50 cc, and phosphate determined absorptiometrically by the molybdate–antimony–ascorbic acid method of Murphy and Riley (1962).

Analytical Checks

To see whether there was any loss of phosphorus in the ignition procedure, a set of nine samples was analyzed, each sample being duplicated, with one of the pair ignited as described above, and the other ignited after being moistened with $MgCl_2$ solution to maintain a basic ash and prevent any possible volatilization of phosphoric acid. The mean of the nine analyses without $MgCl_2$ was 7.61 (μg P per sample) and of the nine with $MgCl_2$ 7.77. This difference is insignificant compared with others shown below.

To see what sort of repeatability could be obtained for the whole procedure, samples were taken (October 22, 1969) from five separate rocks at the same depth (1 m, lake 227) with the following results (micrograms present):

	Mean ± SD	Coefficient of variation
C	4468 ± 790	±17.6%
N	331 ± 64	±19.2%
P	7.60 ± 2.30	±30.2%
Chl. *a*	5.08 ± 0.89	±17.5%

The greater variability of phosphate analyses may be related to the additions of phosphate made during the summer, in the fertilization experiments, and the known rapid and strong absorption of phosphate by plant material.

Algal Cell Counts and Glass Slide Experiments

One of three aliquots was set aside for quantitative counts. Before Lugol's solution was added, the material was examined live (450×) to obtain estimates of percentage composition of major algal groups. Counts of live material were converted to a volume basis using some cell volumes computed by Nauwerck (1963), and others calculated by Stockner and Evans (unpublished data). The relative contribution of each algal group was then expressed as a percentage of the total algal volume present in each sample. Before diatom enumeration, the material was pretreated and mounted on glass slides using methods previously described (Stockner 1968a, b). Diatoms on permanent slides were counted under oil immersion (1000×), using Zeiss-Nomarski differential interference microscopy. The monographs of Hustedt (1930), Cleve-Euler (1951), Patrick and Reimer (1966), Skuja (1964), and Huber-Pestalozzi (1942) were used for algal species identifications.

Glass slides, 2.5 × 7.5 cm, were placed at 1 m depth on a horizontal rock shelf in lake 240. At each sampling interval they were removed, and the accumulated periphyton was scraped off and placed in a vial with a few drops of 10% formalin. The material was filtered on a preweighed Millipore filter (HA 0.45 μ), oven-dried at 105 C, and weighed. Values were then corrected to compensate for millipore filter weight. The periphyton material plus filter were then macerated in concentrated nitric acid and permanent slides were prepared as previously discussed.

At each sampling periphyton was similarly removed on a duplicate slide, dried at 105 C, and burned in a muffle furnace at 500 C to estimate the percentage of ash and organic fractions (loss on ignition (L.O.I.) = organic matter). Biomass estimates were later converted to mg organic (L.O.I.)/cm² or ash-free dry weight for presentation. Quantitative diatom counts in a vertical and horizontal transect were made under 1000× magnification, and results of counts were converted to a cm² basis for presentation.

Results and Discussion

Biological Studies

Species composition

The epilithic algal assemblage received the most intensive study, since rock substrate was dominant in the littoral zone of all lakes examined. Algal species composition was similar in the four study lakes, with diatoms dominating in both numbers and biomass in the epilithic algal community throughout the growing season (Table 1). Common in all lakes, but of less importance in terms of total biomass (volume basis), were filamentous green (Chlorophyta) and blue-green (Cyanophyta) algae. Throughout the period of observation diatoms represented between 60 and 70% of the total volume of epilithic algal biomass, and filamentous green and blue-green algae, together with desmids, accounted for the remainder. There was a marked seasonal pattern within the epilithic assemblage in all lakes. An initial diatom dominance in April and May (80–90% by volume) was followed by a rapid growth of filamentous green algae and desmids (30–40%). From mid-August to mid-September the filamentous blue-greens increased (30–40%), later followed by a second autumnal peak of diatoms (70–80%). This algal succession is similar to that observed in phytoplankton algae in temperate lakes (Hutchinson 1967; Pearsall 1932), and attached algae in streams (Patrick 1948) and lakes (Godward 1937; Flint 1950). Castenholz (1960) observed a similar succession of periphyton algae in freshwater and saline lakes in Washington State, and Fox et al. (1969) noted similar seasonal changes in the epilithic algal communities along the western shoreline of Lake Superior.

The Epilithic Diatom Community — Lake 240

Epilithic diatoms were selected for intensive study because of their dominance in the littoral zone of the study lakes, and the first author's familiarity with their taxonomy and distribution. To date, diatom counts have been completed on one of the four study lakes (lake 240) and these results are reported below.

For a mineralogic description of the dominant rock type along the shoreline and littoral zone, see Brunskill and Schindler (1971).

Seasonal diatom succession — natural rock substrates

There is a well-defined seasonal succession of diatom species in the littoral zone of lake 240 (Fig. 4*a*, *b*), characterized by the vernal abundance of *Fragilaria pinnata*, *Cymbella frigida*, and *Anomoeoneis vitrea*; the midsummer maxima of *Achnanthes minutissima* and *Anomoeoneis serians*; and an autumnal peak of *Fragilaria crotonensis* and *Cymbella tumidula*. Some diatoms showed little seasonal change in relative abundance, notable examples being *Gomphonema angustatum* and *Cymbella microcephala*. *Achnanthes minutissima* was the most common diatom at all sampled depths in the littoral zone, followed in order of abundance by *F. pinnata*, *A. serians*, and *A. vitrea*. *Achnanthes minutissima* was most often found epiphytically, on filamentous green and blue-green algae that

TABLE 1. Common algae identified from the littoral zone of lakes 227, 305, 239, and 240.

Chrysophyta (Bacillariophyceae)

Centrales	Pennales		
	Araphidineae	Biraphidineae	Mono-Raphidioidineae
Cyclotella stelligera Cl. et Grun.	*Tabellaria fenestrata* (Lyngb.) Kütz.	*Anomoeoneis serians* (Bréb.) Cleve	*Achnanthes flexella* (Kütz.) Grun.
Cyclotella glomerata Bachmann	*Tabellaria flocculosa* (Roth.) Kütz.	*Anomoeoneis vitrea* Grun.	*Achnanthes minutissima* Kütz.
Melosira italica (Ehr.) Kütz.	*Fragilaria construens* (Ehr.) Grun.	*Anomoeoneis zellensis* (Grun.) Cleve	*Achnanthes lanceolata* Bréb.
Coscinodiscus subvelatus Schmidt	*Synedra radians* Kütz.	*Navicula radiosa* Kütz.	*Achnanthes grimmei* Krasske
	Synedra delicatissima W. Smith	*Navicula antiqua* A. Bem.	*Eunotia arcus* Ehr.
		Nitzschia fonticola Grun.	*Eunotia elegans* Östrup
		Nitzschia vitrea Norman	*Eunotia pectinalis* (Kütz.) Rabenhorst
		Nitzschia amphibia Grun.	*Eunotia incisa* W. Smith
		Gomphonema angustatum (Kütz.) Rabb.	*Eunotia flexuosa* Kütz.
		Gomphonema montanum Schum.	
		Gomphonema gracile Ehr.	
		Gomphonema acuminatum Ehr.	
		Gomphonema subtile Ehr.	
		Gomphonema intricatum Kütz.	
		Pinnularia microstauron (Ehr.) Cleve	
		Pinnularia mesolepta (Ehr.) W. Smith	
		Pinnularia maior Kütz.	
		Frustrulia rhomboides (Ehr.) de Toni	
		Cymbella ventricosa Kütz.	
		Cymbella microcephala Grun.	
		Cymbella frigida A. Cl.	
		Stenopterobia arctica A. Cl.	
		Stauroneis anceps Ehr.	
		Neidium affine (Ehr.) Cleve	
		Neidium iridis (Ehr.) Cleve	

Chlorophyta	**Cyanophyta**
Rhizoclonium sp.	*Aphanocapsa* sp.
Cladophora sp.	*Chroococcus* sp.
Mougeotia spp.	*Aphanothece* spp.
Chaetophora sp.	*Oscillatoria* sp.
Zygnema spp.	*Dichothrix* sp.
Spirogyra sp.	*Stigonema* sp.
Spondylosium sp.	*Anabaena* sp.
Desmids — several species	*Nostoc* spp.

exhibited maximum densities in the littoral zone in July and August. Cursory examination of the diatoms in the littoral zone of lakes 239, 227, and 305 revealed the clear numerical dominance of *A. minutissima*, followed in order of abundance by *A. serians*, *A. vitrea*, and *Synedra delicatissima*.

Seasonal diatom succession — artificial substrate

The seasonal periodicity of diatom taxa on glass slides placed at a depth of 1 m on a horizontal rock shelf in lake 240 was basically similar to that observed on the natural rock substrates. The only obvious difference was the greater relative abundance of *Cyclotella stelligera* and *Synedra delicatissima* on the glass slides than on the natural rock substrate. Initial colonization of the glass slides was by *C. stelligera* and *A. minutissima*. By the end of May *A. minutissima* was the dominant diatom on the slides, followed in order of abundance by *C. microcephala* and *S. delicatissima*. July counts from both glass slides and rock substrates showed a similar distribution, with *A. minutissima* clearly the dominant diatom on both substrates. In late September and October *A. minutissima* was still numerically dominant but was followed closely in abundance by *Cymbella ventricosa* and *C. microcephala*.

The disappearance of *C. stelligera* from the periphyton in June is of interest, for as pointed out by Stockner (1971), *C. stelligera* is initially common in the littoral periphyton of lake 240 in the spring, but is rapidly removed and becomes common in the phytoplankton in late spring and summer. This phenomenon was referred to by Hutchinson (1961) as one possible mechanism to explain the coexistence of so many ecologically similar phytoplankton species in the relatively homogeneous epilimnetic habitat. Evidence presented here supports this hypothesis.

Godward (1937) noted the unquestioned dominance of *A. minutissima* in her examination of the littoral algae of Windermere, and Fox et al. (1969)

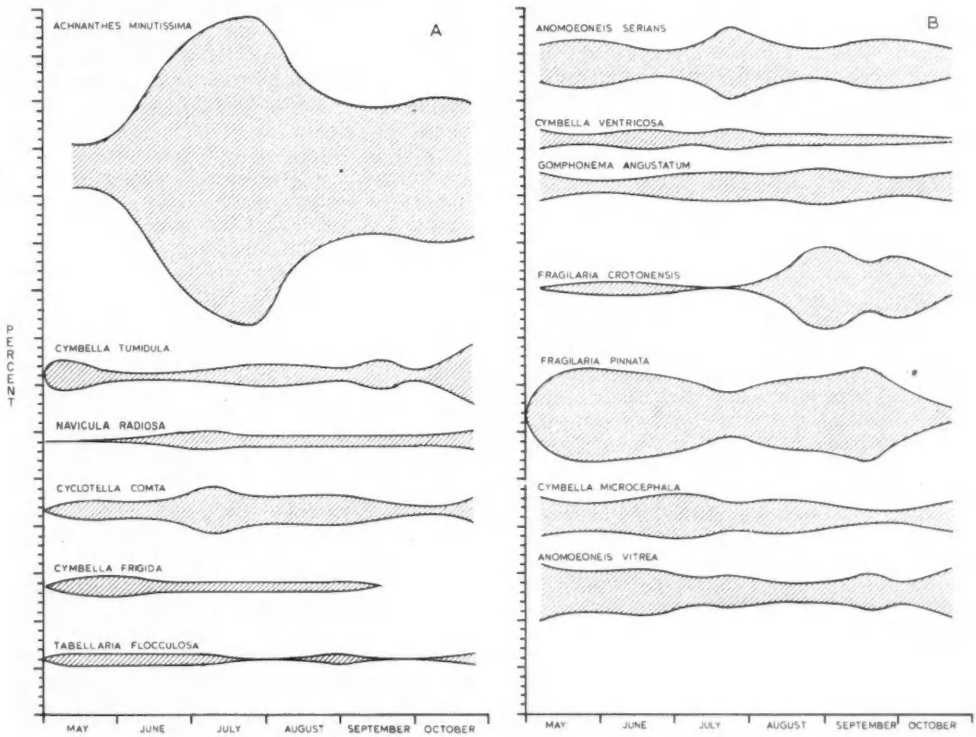

FIG. 4. Seasonal succession of the more common diatoms encountered in the littoral zone of lake 240. The scale is percent relative abundance. Counts from samples from 0 to 5 m in each lake were averaged for each sampling date.

estimated that *Achnanthes* cf. *minutissima* (their *A. microcephala*) at maximum density in August represented 50% of the total diatoms enumerated from the epilithic algae in the littoral zone in western Lake Superior. Clearly, from its observed distribution *A. minutissima* can be considered a reliable character form of the littoral zone of oligotrophic temperate lakes.

Periphyton growth on glass slides

The experimental design did not allow for continuous growth measurements of attached algae on glass slides, since cleaned glass slides were not replaced at each sampling interval. However, it is instructive to compare the observed growth rates during the initial attachment phase, April 22-May 22 (Fig. 5, point *a*), and the period of most rapid growth, May 22–June 18 (Fig. 5, point *b*). The initial period of colonization of the glass slides was not surprisingly characterized by a low growth rate — 27 mg organic matter/m²·day, no doubt attributable to both an initial lag phase and the prevailing low temperatures. From the middle of May to the middle of June very rapid growth occurred on the slides — 250 mg organic matter/m²·day. Estimates of growth on the slides beyond this period are subject to more serious error since factors such as increased respiration, export, and grazing begin to play an increasingly important role — and measurements should more appropriately be considered "accumulated biomass" (Stockner 1968). Total diatoms on the slides increased from 18,000/cm² in May 7, to over 330,000/cm² by June 18. The number of diatoms on the glass slides remained stationary throughout the summer, averaging 250,000/cm², gradually diminishing to roughly 110,000/cm² by late October (Fig. 5), representing increased export losses. The "accumulated biomass" or weight of periphyton on the slides increased gradually from 0.68 mg organic/cm² on June 18, to a maximum of 1.25 mg organic/cm² on September 20, diminishing to 0.70 mg organic/cm² by late October (Fig. 5).

The mean organic content (L.O.I.) was 51 ± 6.6% with little observed seasonal variation. The curves of diatom numerical density and accumulated biomass showed similar patterns up to August where they intersect. This intersection (increased biomass relative to numbers) is a reflection of a relative increase of filamentous green and blue-green algae during this period, which as previously discussed also occurred on the natural rock substrates. In September and October the two curves are again similar, but inverted.

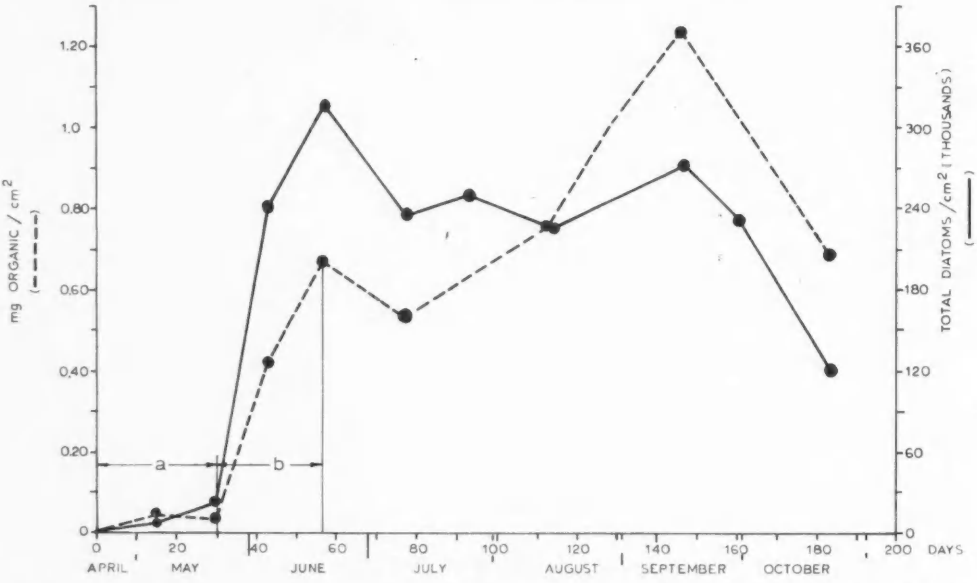

FIG. 5. Changes in total periphyton biomass and diatom density on glass slides at 1 m in lake 240: (*a*) initial colonization period; and (*b*) period of most rapid growth, 30 and 57 days accumulation, respectively.

Counts of diatoms from natural substrates are invariably higher than those recorded from either artificial substrates or denuded natural substrates. This is because both living and dead frustules are unavoidably included in the counts and the total count is thus merely an expression of living and dead accumulated biomass. Total diatom counts of accumulated periphyton diatoms from natural lithic substrates in lake 240 ranged from 300,000 to 1,300,000/cm^2. A similar range of values was recorded by Fox et al. (1969) for Lake Superior periphyton diatoms on lithic substrates. By comparison, counts of attached diatoms on Lake Winnipeg buoys located at the mouth of the Red River in a considerably more eutrophic situation ranged from 5 to 7,000,000/cm^2 (Stockner and Evans unpublished data).

The relative merits of using submerged glass slides to estimate periphyton production are summarily discussed by Castenholz (1960, 1961), Kevern et al. (1966), and Dumont (1969). At this stage of the study and with the limited number of measurements available, results can only be viewed as tentative estimates. The estimate of maximum periphyton growth, 250 mg organic/m^2·day, measured at a depth of 1 m in the littoral zone of lake 240, is similar to maximum rates measured in Falls Lake, Washington, in 1956 by Castenholz (1960) at a depth of 0.4 m, but considerably higher spring growth rates were measured by him on slides placed in the more saline lakes. Using carbon-14 techniques, Wetzel (1964) obtained an average growth rate of over 700 mg/m^2·day in the very alkaline, saline Borax Lake, California. Newcombe (1950) studied the growth of periphyton at various depths in a small lake in Michigan and recorded an average daily growth that was considerably lower than the maximum estimate obtained from lake 240. Daily periphyton growth rates averaging 67 mg organic/m^2 were calculated in Stony Point Bay on the western shore of Lake Superior by Fox et al. (1969). Fox et al. do not give maximum rates that can be directly compared with estimates from lake 240.

After examination of the limited amount of data from the submerged glass slide studies in lake 240, it appears that the spring periphyton diatom maximum occurs, as in the plankton of lake 240, between mid-May and mid-June, followed by increases in filamentous green and blue-green algae in late July and August, and by another smaller autumnal diatom peak in September. The initiation of the spring peak is related principally to nutrient availability, increased light intensity, day length, and to increasing water temperatures (5–14 C). The species complex involved in the spring pulse is generally dissimilar to that in the fall. This is not surprising since different temperature–light regimes prevail. The overall seasonal change in biomass and number on both natural lithic and artificial substrates here compared is generally a function of the combined independent variation of several species. Unfortunately, little is known from other studies about the seasonal periodicity of the particular diatom species encountered in the littoral zone of ELA lakes, and comparison with observation by others on closely related species yields little of value to our overall understanding of littoral algal succession. It is unlikely that a single factor is responsible for the observed seasonal periodicity, and it is probable that an interplay of many factors are involved (Castenholz 1960; Stockner 1968a).

Vertical distribution of littoral diatoms, lake 240

Samples were taken at 1-m intervals to a depth of 5 m in the littoral zone of lake 240. Approximately 2.6% of surface visible radiation penetrates to this depth in lake 240 (Schindler 1971). One percent extinction is at 7–8 m, and it is probable that little attached algal growth occurs on substrates beyond these depths. The variations in standing crop with increasing depth are discussed in the chemical section of this report.

Certain diatom species exhibited a clear vertical zonation in the littoral, and others appear to possess little depth preference, e.g. *A. minutissima*. Four species were selected to illustrate the variability in depth distribution of diatoms in the littoral of lake 240 (Fig. 6). *Anomoeoneis serians* in the spring and fall was most abundant at depths of 1 and 5 m, respectively, whereas during the summer it was more equally distributed at all depths (Fig. 6). *Anomoeoneis vitrea* was most commonly encountered at depths from 0.5 to 3 m and was rarely found at depths greater than 4 m (Fig. 6). *Fragilaria pinnata* was generally more abundant at deeper stations and its distribution was opposite to that observed for *A. vitrea* (Fig. 6). *Cymbella microcephala* was distributed chiefly at depths of from 0.5 to 4 m with greatest abundance at 1 m (Fig. 6).

The observed vertical distribution of diatoms in lake 240 is likely the result of an interplay of both physical and biological factors. Light is the more obvious physical factor, with those species with optimal growth at low light intensities occurring more abundantly in deeper stations, e.g., *F. pinnata*, and those adapted to higher light intensities occurring at shallower depths, e.g., *A. vitrea*. Water temperatures in the littoral are similar to those measured in the epilimnion of lake 240 (Schindler 1971), and therefore vertical temperature differences in the littoral zone are small. One biological factor

affecting the depth distribution of diatoms in the littoral zone is grazing by invertebrates, notably caddisfly larvae and herbivorous gastropods, both of which are common in the littoral zone of lake 240. The importance of invertebrate grazing as a controlling factor in attached diatom distribution is well illustrated by the work of Douglas (1958) and Jansson (1967, 1969).

Psammonal Diatoms, Lake 240

The diatoms associated with sand beaches in lake 240 were given cursory examination. They were usually distributed within the top 5–6 cm of wave-washed sand. Only two diatoms were consistently found with healthy, robust chloroplasts — *Eunotia pectinalis* and *Achnanthes flexella*. They were commonly distributed in the top 2 cm of sand but sometimes were found at a depth of 5–6 cm. Other planktonic and littoral diatom frustules were common on the sand surface, but most were in a state of decomposition. Both *E. pectinalis* and *A. flexella* were rarely observed in the rocky littoral zone of lake 240 and have never been observed in the plankton (S. Holmgren, personal communication). These diatoms are unique to the psammonal habitat of this lake.

Seasonal Chemical Composition of Periphyton

Distribution of C, N, P, and chlorophyll a in periphyton standing stock

The results of chemical analyses on samples obtained on August 28, 1969, were typical data selected to illustrate the variability among lakes in total C, N, P, and chl. *a*/cm² with depth (Fig. 7). In lake 240, there was little variation with depth for all components, but in lake 239, maximum values occurred at 2–3 m. In contrast to lake 239, lake 305 showed highest concentrations of all components at the surface and at 5 m (Fig. 7). Lake 227 showed maximum values of C and N at 3 m, chl. *a* at 2 m, and P at 1 m. Much of the

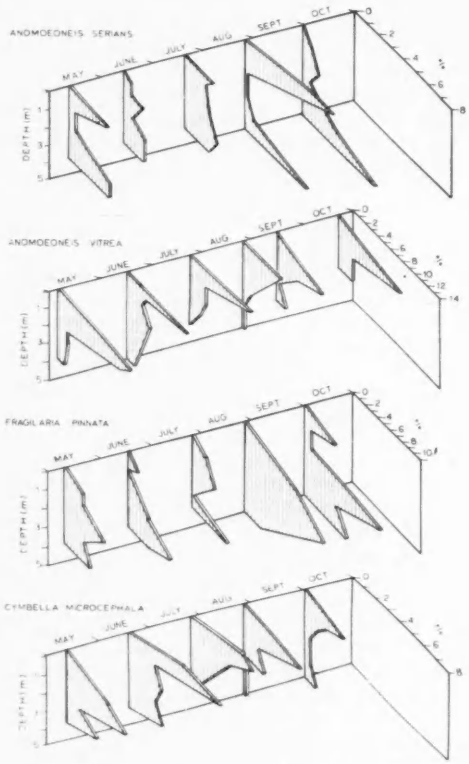

Fig. 6. Seasonal change in the vertical distribution of four common littoral diatoms in lake 240. Samples were obtained from natural rock substrates.

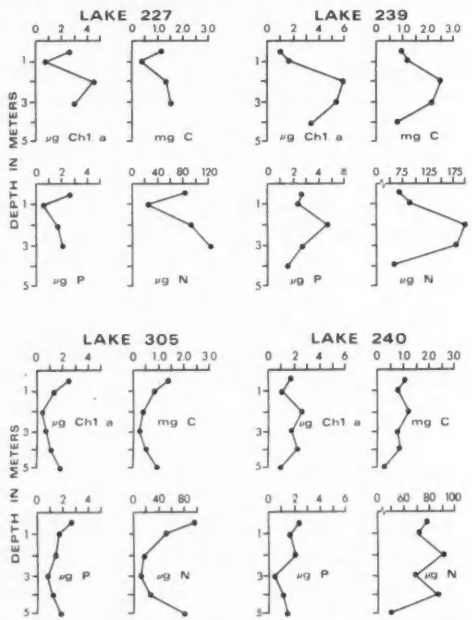

Fig. 7. Vertical distribution of C, N, P, and chl. *a* on August 28, 1969, in the four study lakes. Values are per cm².

observed depth variation in C, N, P, and chl. *a* in periphyton standing stock is attributable to variation in growth at given depths that is in turn related to light penetration (see Schindler 1971). Grazing by either herbivorous insects, gastropods, or larval stages of *Rana* and *Bufo* is also an important regulator of specific amounts of accumulated biomass at given depths. Larval stages of *Rana* and *Bufo* are common in July and August in the littoral zone of most ELA lakes, sometimes reaching densities of between 10 and 13 individuals/m^2. Examination of their gut contents revealed an exclusive diet of periphyton. Fox et al. (1969) attributed observed depth variations in accumulated periphyton biomass along the western shore of Lake Superior to currents, especially in shallow (0–2 m) stations, where strong wave wash during storms removes much of the periphyton growth. Though no doubt of considerable importance in the Great Lakes, wave wash is probably only of significance in the shallower (0–50 cm) splash zone of the ELA lakes. The seasonal variation in specific amounts of C, N, P, and chl. *a* observed in the study lakes was similar to changes in accumulated biomass in lake 240 as plotted in Fig. 5. The seasonal variation of total P with depth in lake 240 illustrates the basic pattern observed in all study lakes (Fig. 8). High concentrations were recorded in late May and early June, minimum values during July and August, and highest concentrations in September.

A canonical analysis (Seal 1964) was performed to identify and sort out differences among lakes in the distribution of total N, P, and chl. *a*/cm^2 in periphyton standing stock (Fig. 9A–C). Total C was not included because the sample size was too small (<30/lake) to meet the requirements of the test. The number of samples obtained from the littoral of each lake varied, but in all instances exceeded 50/lake. Amounts of N among lakes, and among depths within lakes, were not significantly different; however, specific amounts of P and chl. *a* among lakes tested were significantly different ($P = 0.01$) (Fig. 9A and C). Though not significantly different, the highest concentrations of both P and chl. *a* were generally at shallower depths, 1–2 m. Seasonal comparisons of the relation between P and chl. *a* in the four lakes showed much

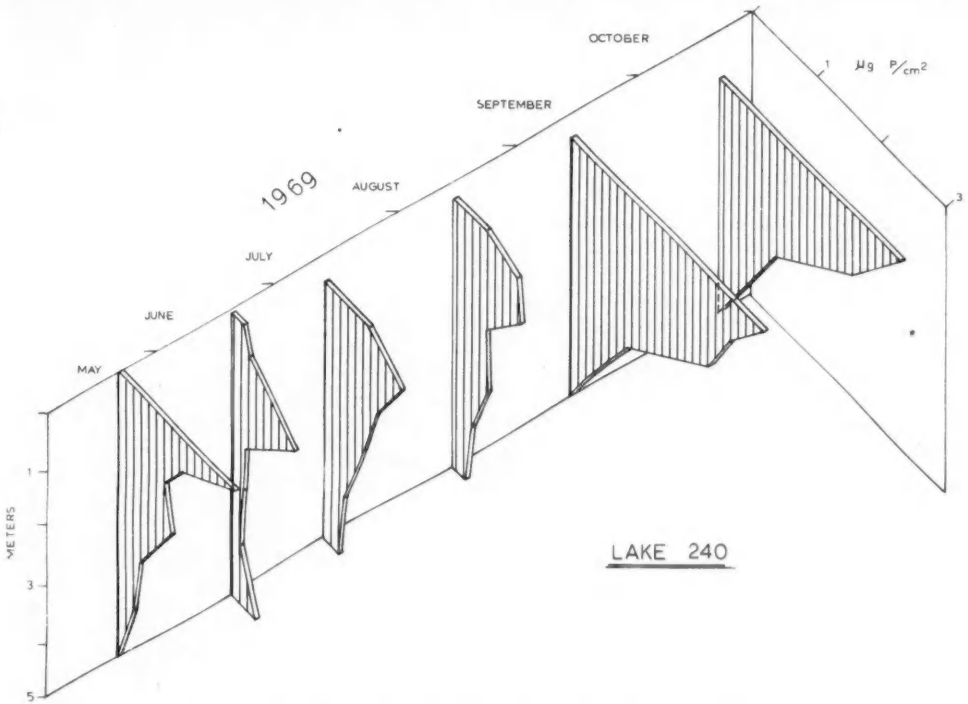

FIG. 8. Seasonal variation in total P, in littoral standing stock, lake 240.

greater concentrations of chl. *a* relative to P (chl. *a* > P) in the spring and the opposite relation (P > chl. *a*) in the fall (Fig. 9A). These results show that at the initiation of the spring pulse, stored P is rapidly utilized to produce the observed substantial increases in periphyton standing stock, i.e., chl. *a* > P. The opposite occurs in the fall, greater storage of P in relation to much smaller increases in standing stock, i.e., P > chl. *a*. This seasonal relation was particularly noticeable in lake 227, the lake receiving weekly additions of N and P.

Observed differences among lakes can also be seen by plotting the mean values of P and chl. *a* on a relative scale (Fig. 9B). Lake 239 seasonally had the highest concentrations of both components, followed in order of decreasing abundance by lakes 227, 305, and 240. Lake 239 periphyton on the average contained approximately one-third again as much P and chl. *a* as did lake 240; and lake 227, enriched with N and P additions, surprisingly contained slightly less P and chl. *a* than lake 239. It is likely that without weekly additions of N and P, lake 227 would have ranked much lower on the scale, perhaps as the lowest in the series. With further additions of N and P planned for 1970–71, lake 227 will in all probability surpass lake 239 in concentrations of all components in

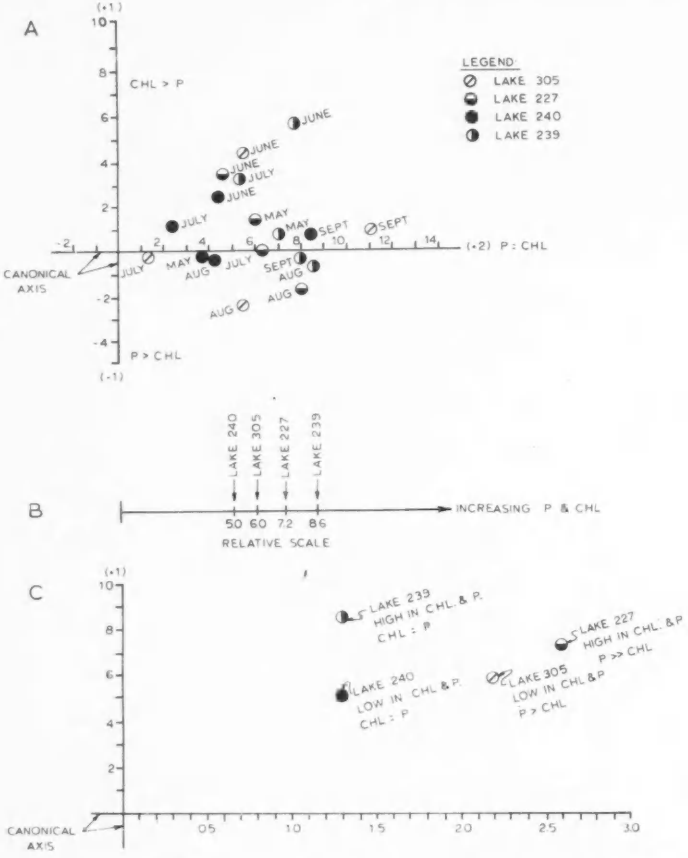

FIG. 9. Results of a canonical analysis of chemical analyses of periphyton standing stock in the four study lakes. A, Seasonal changes in amounts of chl. *a* and P in the periphyton; B, ranking of lakes in relation to increasing amounts of chl. *a* and P; and C, the interrelation between specific amounts of chl. *a* and P between lakes.

the periphyton, since samples taken in October contained about twice as much P/cm² as in the other lakes (Table 2). Further indications of the lake's response to fertilization is seen by comparing the ratio of the average September and October sample values of N to P in the periphyton (12:1) to the average in the other lakes (40:1).

Additional ecological information can be obtained by comparing the seasonal variation of total N and P in periphyton biomass in each lake when expressed as a percentage of periphyton organic weight (mg)/cm² (Table 2). There was no significant difference observed in total N content of periphyton in all study lakes, averaging between 2.4 and 2.6% (*t*-test, $P = 0.05$). In lake 227 a substantial increase was noted, rising to 7.6% in the middle of August, approximately 50 days after the commencement of fertilization. By September, however, the measured values of N were similar to those observed in the other lakes. The seasonal average N content of periphyton was similar in lake 239 and 240, about 2.6%, lowest in lake 305, 2.3%, and highest in lake 227, about 3.1%.

Amounts of total P were low in all lakes except lake 227 in June and early July, about 0.02–0.05%, levelling off for the remainder of the summer and early fall at about 0.08% (Table 2). Periphyton in lake 227 showed the greatest concentrations of total P, reaching 0.34% on July 8, and remaining consistently higher than values observed in the other lakes. The seasonal averages were similar for lakes 239, 240, and 305 (between 0.04 and 0.06%), but significantly higher in lake 227 (0.15%) (*t*-test, $P = 0.05$).

Observed increases in concentrations of total N and P in the periphyton of lake 227 are likely the result of "luxury consumption," a phenomenon often observed in algae and higher plants when grown in an environment enriched with N and P (Gerloff and Skoog 1954; Fitzgerald 1969). The abrupt increase and rapid decline in the concentration of N in periphyton in lake 227 is puzzling because the lake received weekly additions of both N and P for the duration of the summer in 1969, and NO_3-N in the epilimnion rose steadily (F. A. J. Armstrong unpublished data). The same general pattern observed in the periphyton was also noted in the total N content of the 0–1-m seston in lake 227 (F. A. J. Armstrong, unpublished data.) If, as shown by the experiments of Gerloff and Skoog (1954), the tissue content of the element can continue to rise with increasing external concentrations, then it is surprising that concentrations of N in the periphyton did not increase and remain at concentrations considerably greater than observed in the other lakes. Amounts of total P in the periphyton of lake 227 varied considerably, but basically showed a pattern consistent with the observations of Gerloff and Skoog (1954).

Gerloff and Skoog (1954) and Fitzgerald (1969) have noted from laboratory experiments that a fairly definite concentration of both elements (critical levels) must be maintained to sustain optimal growth, and that tissue or cellular concentrations may continue to increase beyond the critical level with no appreciable effect on growth (luxury consumption). They have established critical levels for a variety of Angiosperm aquatic plants and a blue-green alga *Microcystis aeruginosa* in laboratory experiments. Lund (1950) has summarized available data on cell concentrations of N and P in *Asterionella formosa*, and though not

TABLE 2. Average concentrations of nitrogen and phosphorus in periphyton taken at a depth of between 0.5 and 1.0 m in each of the study lakes. Values are percent of N and P/mg organic wt.

	Lake 239		Lake 240		Lake 305		Lake 227	
	% N	% P	% N	% P	% N	% P	% N	% P
May 22	2.82	0.09	2.66	0.07	–	–	–	–
June 19	2.84	0.02	2.52	0.03	2.23	0.001	2.26	0.004
July 8	2.29	0.02	2.76	0.03	2.53	0.05	2.03	0.34
July 24	2.28	0.009	2.64	0.01	2.38	0.007	2.89	0.007
Aug. 14	2.71	0.05	1.91	0.07	2.21	0.06	7.62	0.24
Aug. 28	2.44	0.08	2.80	0.14	2.20	0.08	2.59	0.08
Sept. 15	2.41	0.09	2.39	0.07	2.04	0.06	2.28	0.22
Sept. 30	2.72	0.09	3.02	0.09	2.44	0.04	2.96	0.11
Oct. 22	2.79	0.05	2.64	0.06	–	–	2.46	0.21
Avg	2.59	0.06	2.59	0.06	2.29	0.04	3.14	0.15

stated as critical concentrations, provide a more realistic comparison in light of the diatom dominance in the periphyton of ELA lakes. Though critical levels have not been established from laboratory culture of periphyton (such studies are currently in progress), it is nonetheless instructive to make such comparisons to see whether values obtained in this study are below Lund's (1950) average values and Gerloff and Skoog's (1954) established range of critical concentrations. Such comparisons may indicate nutrient limitation, or conversely "luxury consumption," that would suggest a surplus of N and P in the ELA lakes. The "critical concentration" of N and P established for *M. aeruginosa* was 4.0 and 0.20% respectively (Gerloff and Skoog 1954) and average values for *Asterionella formosa* 3.0 and 0.10% respectively (Lund 1950).

Values of N in the periphyton of lake 227 reached a concentration of 7.6% in the August 14 sample, but with this exception, in all lakes including lake 227, values were below the 3.0–4.0% figure. However, concentrations of P in the periphyton of lake 227 exceeded the 0.10–0.20 critical range on five of the eight occasions samples were taken (Table 2). Results of these comparisons suggest that amounts of P in lake 227 after fertilization were sufficient to sustain optimal growth but that other nutrients, perhaps N, CO_2, or trace metals, limited periphyton growth in this lake. The other study lakes, however, likely contain suboptimal amounts of both N and P that accordingly may be limiting periphyton growth. Hopefully, results of periphyton bioassay experiments currently in progress will test this conjecture and elucidate which nutrient(s), and at what external concentrations, are regulating periphyton growth in ELA lakes.

Acknowledgments

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Crustacean Plankton Communities in Forty-Five Lakes in the Experimental Lakes Area, Northwestern Ontario[1]

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PATALAS, K. 1971. Crustacean plankton communities in forty-five lakes in the Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Bd. Canada 28: 231–244.

Zooplankton communities were characterized on the basis of samples taken in summer as vertical net hauls in the central part of lakes. Twenty-eight species of crustaceans were found in the 45 lakes studied. The highest number of species as well as the highest numbers of individuals (per unit of area) usually occurred in the largest deepest lakes with most transparent water.

The most common species were: *Bosmina longirostris*, *Tropocyclops prasinus mexicanus*, *Mesocyclops edax*, *Diaptomus minutus*, *Holopedium gibberum*, and *Cyclops bicuspidatus thomasi*. Daphnids were rather scarcely represented.

Senecella calanoides, *Limnocalanus macrurus*, and *Diaptomus sicilis* were confined to rather deeper lakes, whereas *Diaptomus oregonensis* was found mostly in smaller shallower lakes and *Diaptomus leptopus* in very small, but relatively deep lakes. *Diaptomus minutus* and *C. b. thomasi*, though widely distributed, showed a preference for deeper lakes, whereas *T. p. mexicanus* tended towards smaller shallower lakes.

In particular lakes, the number of dominants ranged between 1 and 5, but three dominants per lake was the most commonly encountered case. The simplest community was composed of one cyclopoid, though the most common consisted of one cyclopoid, one diaptomid, and one cladoceran.

Four types of communities were distinguished, each of them characteristic for a group of lakes of specific size and depth: (I) in the largest and deepest lakes (389–1007 ha of area, 30–117 m maximum depth); (II) in lakes of medium size and depth (6.5–200 ha, 4.8–33 m); (III) in small and very shallow lakes (3.1–28 ha, 2.7–7.3 m); (IV) in very small lakes with medium depth (1.3–3.7 ha, 6.1–12.8 m).

The high degree of similarity between the plankton communities of the Experimental Lakes Area (ELA) and southern Ontario, as well as of some Great Lakes, suggest that they all basically belong to the same zoogeographical area.

The fact that most species were distributed evenly throughout ELA may indicate the relative uniformity of the area. In ELA, lake morphology is mainly responsible for defining the type of community.

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ANY attempt to generalize the interrelation between the types of aquatic environments and their plankton communities faces the lack of substantial information on regional differences. This is especially valid in the case of Canadian lakes, distributed over a vast area of different geological regions and climatic zones. A comparison of previous studies by Carl (1940) on British Columbia lakes, Rawson and Moore (1944), Moore (1952), Reed (1964), and Anderson (1967) on Saskatchewan and Alberta lakes, and Langford (1938), Rigler and Langford (1967), and Robertson (1966) on Ontario lakes points out the apparent regional differences. Although many records of the occurrence of the particular species or groups of species in single lakes in different provinces exist, the information is too scarce to determine whether or not there are some characteristic communities for lakes of various types. The main purpose of this work was to provide an answer to such a question applied to a group of 45 Experimental Lake Area (ELA) lakes before the commencement of enrichment experiments. Two approaches were undertaken in the interpretation of the zooplankton data: (1) the characterization of species, in terms of ecological requirements; and (2) the characterization

[1]The ninth in a series of 14 papers on the work of the Fisheries Research Board of Canada, describing background environmental data on the Experimental Lakes Area, northwestern Ontario. For location of numbered lakes see insert map at the back of this issue of the Journal of the Fisheries Research Board of Canada. A key to lake locations is given by Cleugh and Hauser (1971).

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of the lakes on the basis of their planktonic communities.

Methods and Materials

The lakes selected for study ranged from 1.3 to 1007 ha in area and from 2.7 to 117 m in maximum depth (Brunskill and Schindler 1971; Cleugh and Hauser 1971). They have total dissolved solids (TDS) values ranging from 10 to 90 ppm (Armstrong and Schindler 1971; Cleugh and Hauser 1971). Secchi disc visibility measured during the summer varied from 1.0 to 10.7 m. The detailed characteristics of each lake are presented in Table 1.

TABLE 1. Percentage composition of crustacean species in the

Lake	Date	Area (*ha*)	Max depth (*m*)	Color pt (*ppm*)	Secchi disc visibility (*m*)	TDS (*ppm*)	Chl. *a* (*μg/liter*)	Zooplankton: Total no. indiv. per cm³	Zooplankton: Total no. species	Zooplankton: Community type	*Senecella calanoides* Juday	*Limnocalanus macrurus* Sars	*Epischura lacustris* Forbes	*Diaptomus sicilis* Forbes	*Diaptomus minutus* Lilljeborg	*Diaptomus oregonensis* Lilljeborg	*Cyclops vernalis* Fischer
161	6.8.68	1007	>117	5	10.7	20	.5	71	10	I	.1	.2	.2	<.1	24.6		
464	6.8.68	770	37	18	6.4	27	1.2	47	13	I		.1	1.2	5.0	25.9		
254	6.8.68	388	>30	10	5.9	60	2.2	79	14	I	.5	<.1	.1		25.6		6.3
305	5.7.68	52.0	32.7	8	6.8	20	.8	39	9	II			.2	2.0	48.1		
239	5.7.68	56.1	30.4	20	4.2	20	1.8	34	9	II			.5		30.3		
465	7.8.68	200	30	12	7.1	26	1.3	71	9	II					14.4		
256	9.8.68	120	22.4	5	8.8	30	20.0	46	9	II			1.6	43.4?	33.4		
265	28.9.67	13.1	18.6	12	4.5	30		12	7	II			2.0		60.5		
265	6.7.68				4.2			31	6	II			.6		44.2		
251	15.8.68	100	17.3	12	5.6	90	2.4	54	9	II					10.8		
224	27.9.67	25.4	16.7		7.0	40		11	11	II(?)			3.5	32.3	39.4	.7	
189	7.8.68	28.8	15.8	10	5.9	20	4.2	46	10	II			1.2		18.3		1.4
240	5.7.68	44.1	13.1	25	4.1	20	1.6	6	8	II			2.8		31.2		1.3
122	8.8.68	12.2	12.8	18	5.8	35	3.0	31	8	II			4.3		63.6		
226	27.9.67	21.8	12.2		4.2	40		10	10	II(?)			.8	<.1?	52.1		
223	27.9.67	30.2	11.2		5.0	40		6	10	II			.7		54.7	.7	
67	15.8.68	15.1	10.8	45	3.1	20	3.0	21	9	II/III					25.2	1.8	
227	28.9.67	5.0	10.0	18	2.6	60	18.0	18	11	II/III			1.1		58.9		
227	5.7.68				2.6		3.1	49	10	II			.4		39.1		.1
163	8.8.68	15.7	8.5	15	4.4	40	3.3	46	10	II			.8		13.6		1.2
132	16.8.68	7.2	8.4	15	3.7		2.0	26	9	II/III/IV					37.3		
99	9.8.68	6.5	7.6	25	2.2	15	6.5	22	10	II			1.6		12.2		
257	9.8.68	28.2	7.6	50	3.5	20	3.0	26	6	II/III						51.8	
69	15.8.68	15.7	7.3	55	1.8	30	7.7	21	8	III			.1			9.4	
304	5.7.68	3.6	6.7	20	3.0	40	6.1	12	8	II/III					44.0		
164	8.8.68	15.3	6.6	50	3.7	50	3.5	14	11	II/III					5.1	2.7	30.2
233	28.9.67	2.8	6.1		1.0	20		6	8	II/III					19.8	.1	
152	14.8.68	5.3	6.1	20	2.5	10	0.9	21	7	III						11.3	
248	28.9.67	6.5	5.4		1.4	20		42	10	II/III					.1		
222	27.9.67	17.5	5.4		2.2	30		3	10	III					2.4	9.5	
221	27.9.67	8.9	5.4		3.0	20		21	14	III			.1		10.1	24.4	
127	14.8.68	4.7	5.2	20	3.1	23	2.7	22	4	II/III					65.0		.8
165	8.8.68	11.4	4.8	35	3.5	30	2.4	12	9	II/III					7.1	.7	
149	14.8.68	28.0	4.2	18	2.5	10	3.3	16	9	III						12.8	
82	14.8.68	9.9	4.0	110	1.5	63	9.0	15	8	III						20.9	16.8
162	9.8.68	4	3.6	18	2.7	40	3.5	4	4	II/III			21.3		59.4		23.4?
229	28.9.67	3.1	3.6		2.9	40		8	7	III			.1			22.1	
70	15.8.68	11.1	3.5	65	1.2	30	31.0	16	6	III						15.8	
220	27.9.67	4.2	3.3		3.3	30		6	9	II/III			.9		38.5	.9	.1?
150	14.8.68	11.8	2.7	25	2.3	20	2.0	4	5	III			.5			55.5	
230	28.9.67	1.7	12.8	25	5.1	40	25.0	10	8	IV						2.8	
230	5.7.68				4.9			9	6	IV							.1
241	28.9.67	1.8	12.5	65	3.3	10		3	5	IV							7.7
241	5.7.68				2.0			6	6	IV							
8	12.8.68	3.2	12.2	10	6.5	40	3.3	14	5	IV					2.5		
235	28.9.67	2.8	8.2		1.2	10		6	8	IV					.1		
95	9.8.68	3.7	7.6	140	1.3	38	2.4	12	5	IV							
81	22.7.68	1.3	7.0	90	2.0	35	21.0	2	6	IV							
234	28.9.67	1.5	6.1		1.2	10		2	8	IV					7.9		

[a]Question marks after some figures denote instances where identification to the species level was probable but not certain.

In 1968 plankton samples were obtained during the daylight hours by a series of vertical hauls from near the lake bottom to the surface using a modified Clarke-Bumpus sampler with No. 15 bolting silk (mesh size 90 μ) pulled up with the speed of 0.3–0.5 m/sec. During September 1967 samples were taken with a large Wisconsin net (mouth diameter 25 cm, mesh size 90 μ). Crustacean abundance was expressed as the number of specimens per cm² of lake area, based on the assumption that the filtration efficiency of the net was 100%. The data presented should not be interpreted as true densities but rather as relative abundance values proportional to densities, since the nets' true efficiency probably varied from 40 to 50% (Rawson 1956). De-

of 45 ELA lakes and some limnological features of these lakes.

Diaptomus oregonensis Lilljeborg	*Cyclops vernalis* Fischer	*Mesocyclops edax* Forbes	*Tropocyclops prasinus mexicanus* Kiefer	*Orthocyclops modestus* (Herrick)	*Daphnia longiremis* Sars	*Daphnia retrocurva* Forbes	*Daphnia galeata* Sars *mendotae* Birge	*Daphnia galeata mendotae* (× *thorata* Forbes)	*Daphnia catawba* Coker	*Daphnia schoedleri* Sars	*Daphnia pulex* Leydig	*Ceriodaphnia lacustris* Birge	*Ceriodaphnia pulchella* Sars	*Bosmina longirostris* (O. F. Müller)	*Chydorus sphaericus* (O. F. Müller)	*Holopedium gibberum* Zaddach	*Diaphanosoma brachyurum* (Lievin)	*Diaphanosoma leuchtenbergianum* Fischer	*Leptodora kindtii* (Focke)	*Alona intermedia* Sars	*Streblocerus serricaudatus* (Fischer)
							2.3							7.4		.1			.04		
	6.3	4.2				2.3								17.4	3.5	3.8		7.7?	.01		
		2.3	1.2		.9	.9	.9							4.4	1.6	.7	3.0?*				
		1.1					5.6							.9		.1	<.1				
		1.6	.3				1.1							3.2		.1		.3?			
		<.1	2.3			4.9							<.1	5.1	.8			3.3			
		.4						5.2								.4	.8		.02		
			13.2			1.1?								2.0				.2			
			1.6											1.7				.1			
.7		2.2	1.2				1.5							9.8	6.2	4.2	3.8?				
	1.4	1.5						12.9						6.5				.2	.02		
	1.3		10.9			.6	.2							.4		.8		2.4?			
		11.2	11.2				14.3							2.8		8.6					
					1.6		3.7							2.4				9.8	.01		
.7		5.0	16.7			11.2								8.1		3.9					
1.8		.7	14.8					5.5						4.8		.7		4.1			
		24.8	18.7			4.4								5.2		4.4	10.5				
	.1	.3	31.7	.1		1.8								4.1		.1		<.1			
	1.2	.9	4.0			.1								7.1		4.5		1.1			
		3.0	.6			21.1	5.2		13.5?					.2				.2	.20		
		8.4	8.8											1.8		1.4		17.0			
51.8		20.3	21.9	21.9			<.1									.1		.1	.04		
9.4		3.9					14.9							1.7			2.6				
		22.7	48.9			.8								7.7				10.2	.10		
2.7	30.2	15.0	1.0											2.9		1.4	2.9?				
.1		32.9	11.4			5.2			.1			.1		5.2		22.2	.6?				
11.3		10.8	49.7	1.3		.7								17.2		.2					
		24.1	38.5											11.3	1.7	5.2		7.8			
9.5		.1	87.3			.6								2.3	<.1	.6	<.1			.004	
24.4		16.9	22.0			2.4						.1		17.8		27.3	.1				
	.8	3.0	9.2			15.9						.1		21.3	.1	8.1		.2			
.7		8.7	3.0															22.5			
12.8		47.9	11.4			10.9						4.5		.4		16.3		1.4			
20.9	16.8	8.8	21.5									1.5		24.3	.6	13.7		1.7			
	23.4?	20.2	18.1									1.2		7.4		8.0	.1				
22.1			17.1															2.1			
15.8		1.1	66.8			.2	<.1							9.7							
.9	.1?	50.7	.1						5.2					28.1							
55.5			.9					8.3						.9		28.5		1.8			
2.8			40.1											3.9		.1					.1
	.1		85.6							<.1				7.3		.4	1.2?				
	7.7		7.8											11.8		5.9	31.4				
			88.1	3.0										.6			2.5				
			12.8	19.7										1.1		2.2	15.0				
		1.3		85.8					.1?					10.2							
		.2	92.0								<.1?			2.8		.3	.2				
			58.4						.8?					.1			26.7				
				12.0						9.5?				2.4		3.4	1.4?				
		8.5	28.5								1.3?			7.9		21.2	.7				

pending on its size, each lake was sampled at one to three stations. As a rule, the results relate to the station nearest the lake center. Fifteen lakes were sampled in September 1967, 9 lakes in July 1968, and 25 lakes in August 1968. Basically, each lake was sampled once, with the exception of four lakes that were sampled twice: in September 1967 and in July 1968.

Results

Table 1 gives the limnological characteristics of the lakes investigated and the percentage composition of crustacean species. The lakes are arranged according to their maximum depth, the only exception being a group of seven very small lakes (area 1.3–3.7 ha) that appears at the end of the list.

In all, 28 species of crustaceans were found. Of these, 26 can be considered as pelagic and two as littoral forms (*Alona intermedia* and *Streblocerus serricaudatus*). In addition, a form of *Daphnia galeata mendotae* was found with some features resembling *Daphnia thorata*. From 4 to 14 species coexisted within a single lake. The greatest number of species was usually found in lakes of larger size; a simple correlation between the lake area and the number of species showed significance at the 1% level ($r = 0.52$, Table 3).

In Table 2, the species are arranged according to the frequency of their occurrence. Also, the number of lakes in which a single species contributed more than 10% of the total number of crustaceans is indicated (such species were termed "dominants"). The most common species was *Bosmina longirostris*, which occurred in 91% of lakes; however, it was a dominant only in 18% of lakes.

Tropocyclops prasinus mexicanus, *Mesocyclops edax*, *Diaptomus minutus*, *Holopedium gibberum*, and *Cyclops bicuspidatus thomasi* were found

TABLE 2. Frequency of occurrence of particular species of crustacean zooplankton in 45 ELA lakes.

Species	No. lakes in which the species occurs	%	No. lakes in which the species occurs as a dominant (i.e., more than 10% of all crustaceans)	%
Bosmina longirostris	41	91	8	18
Tropocyclops prasinus mexicanus	36	80	25	55
Mesocyclops edax	34	75	12	27
Diaptomus minutus	33	73	26	58
Holopedium gibberum	31	69	6	13
Cyclops bicuspidatus thomasi	27	60	18	40
Epischura lacustris	22	49	1	2
Diaphanosoma leuchtenbergianum	20	44	3	7
Diaptomus oregonensis	18	40	8	18
Diaphanosoma brachyurum	17	38	1	2
Daphnia retrocurva	16	35	4	9
Daphnia galeata mendotae	16	35	3	7
Cyclops vernalis	10	22	3	7
Diaptomus leptopus	8	18	3	7
Chydorus sphaericus	8	18	0	0
Leptodora kindtii	8	18	0	0
Orthocyclops modestus	7	16	3	7
Diaptomus sicilis	6	13	2	4
Ceriodaphnia lacustris	6	13	0	0
Daphnia catawba	5	11	1	2
Limnocalanus macrurus	3	6	0	0
Senecella calanoides	2	4	0	0
Daphnia longiremis	2	4	0	0
Daphnia schoedleri (?)	2	4	0	0
Daphnia pulex	2	4	0	0
Ceriodaphnia pulchella	1	2	0	0
Alona intermedia	1	2	0	0
Streblocerus serricaudatus	1	2	0	0

TABLE 3. Correlation between lake area, maximum depth, color of water, Secchi disc visibility, and the relative abundance of zooplankton species. Calculated after logarithmic transformation. Forty-four degrees of freedom for area, depth, and Secchi disc, 32 df for color. Significant correlation at the 1% level is underlined with a solid line and at the 5% level with a broken line

	Area (*ha*)	Max depth (*m*)	Color (*ppm*)	Secchi disc visibility
Area (*ha*)	·	0.70	−0.54	0.66
Max depth (*m*)	0.70	·	−0.57	0.74
Color (*ppm*)	−0.54	−0.57	·	−0.82
Secchi disc visibility	0.66	0.74	−0.82	·
Cyclops bicuspidatus thomasi	0.66	0.66	−0.58	0.63
Diaptomus sicilis	0.46	0.33	−0.59	0.41
Diaptomus minutus	0.38	0.44	−0.63	0.52
Daphnia galeata mendotae	0.33	0.32	−0.32	0.33
Mesocyclops edax	−0.42	−0.37	0.01	−0.34
Diaptomus oregonensis	−0.10	−0.53	0.47	−0.30
Diaptomus leptopus	−0.44	−0.09	0.40	−0.39
Tropocyclops prasinus mexicanus	−0.53	−0.44	0.22	−0.59
Total no. individuals	0.65	0.56	−0.57	0.52
Total no. species	0.52	0.38	−0.36	0.30

in 60–80% of the lakes. None of the remaining species occurred in more than 50% of the lakes. Daphnids were not as common as copepods in the lakes under consideration and rarely reached greater numerical abundance. The most common daphnid, *Daphnia retrocurva*, was found in 35% of the lakes but it was a "dominant" only in 9% of the lakes.

In Fig. 1–3 frequency distribution histograms of particular species in lakes of different character are presented. Each histogram, differentiated into four quantitative categories, denotes a certain physical aspect of the lakes under study.

Senecella calanoides and *Limnocalanus macrurus* were caught only in the largest deepest lakes. *Diaptomus sicilis* was mostly found in large deep lakes but it also was taken from a few lakes of medium size. *Epischura lacustris* and *D. minutus* occurred in lakes of all types, but apparently preferred the transparent water in deep lakes. *Diaptomus oregonensis* showed a tendency to be limited to small shallow lakes with low transparency. It was not found in lakes over 100 ha or deeper than 20 m with a Secchi disc visibility greater than 7 m. *Diaptomus leptopus* occurred predominantly in very small lakes with areas from 1 to 9 ha but

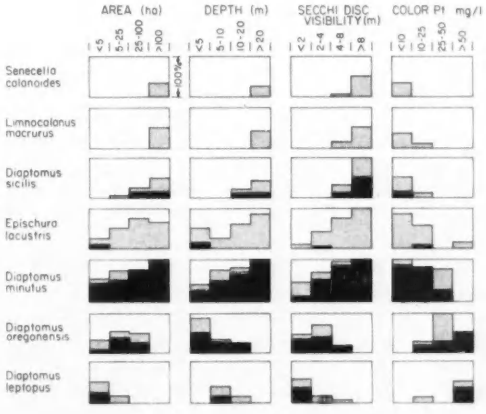

FIG. 1. Frequency distribution of calanoids in ELA lakes of different area, depth, water transparency, and color. The height of vertical bars corresponds to 100% of lakes of a particular category. The shaded part of the bar refers to the percentage of lakes in which that species occurred. The height of the solid bar indicates the percentage of lakes in which the species was dominant (accounted for more than 10% of all crustaceans).

with relatively deep water (5.4–12.8 m). As a rule, these were lakes with highly colored water and low transparency. It is noteworthy that this species was not found in very shallow lakes. *Cyclops bicuspidatus thomasi* (Fig. 2) occurred in large, deep, transparent waters and was rarely found in the smallest shallowest lakes. *Mesocyclops edax* and *T. p. mexicanus*, although present in all lake types, were more frequently abundant in smaller lakes of shallow to medium depth, low to medium transparency, and highly colored waters. *Cyclops vernalis* and *Orthocyclops modestus* occupied an intermediate position with some tendencies toward small shallow lakes. *Daphnia longiremis* (Fig. 3) was found in only two lakes of medium to large size with transparent slightly colored water. *Daphnia galeata mendotae*, although present in all types of lakes, occurred more frequently in larger, deeper, and more transparent waters. The remaining cladocerans *Leptodora kindtii*, *D. retrocurva*, *Chydorus sphaericus*, *Diaphanosoma leuchtenbergianum*, *Diaphanosoma brachyurum*, *B. longirostris*, and *H. gibberum* were present in all types of lakes. However, *H. gibberum* was abundant only in shallower lakes with highly colored waters of low transparency. The relation between certain lake characteristics and the relative abundance of a particular species was also investigated, applying a simple correlation analysis to data that had been transformed logarithmically (Table 3). In addition, it appeared that the lake characteristics are, with the exception of the concentration of chlorophyll *a*, significantly correlated among themselves. A significant correlation at the 1% level was found between lake area and maximum depth, lake area and Secchi disc visibility, maximum depth and Secchi disc visibility, color and maximum depth, and color and Secchi disc visibility. Thus, maximum depth and Secchi disc visibility tend to increase whereas color tends to decrease with increasing lake area. These limnological features of ELA lakes subsequently served as an appropriate background for the interpretation of the results of the crustacean plankton analysis.

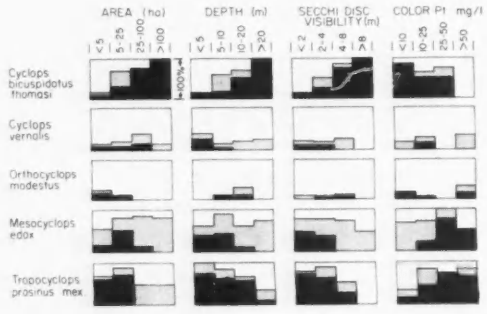

FIG. 2. Frequency distribution of cyclopoids in ELA lakes of different area, depth, water transparency, and color (see legend, Fig. 1).

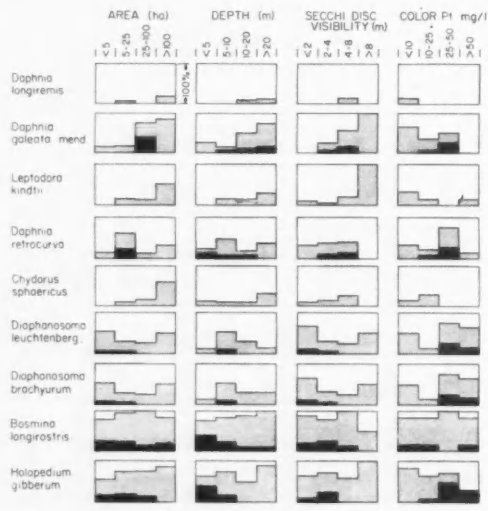

FIG. 3. Frequency distribution of cladocerans in ELA lakes of different area, depth, water transparency, and color (see legend, Fig. 1).

In Table 3, only species that were found frequently enough were considered. The correlation coefficients generally confirm the frequency distribution pattern as presented in Fig. 1–3.

The total numbers of plankters, though derived in a semiquantitative way, can at least be compared amongst individual lakes. Numbers were positively correlated at the 1% level with area, maximum depth, and Secchi disc visibility, and negatively correlated at 1% level with water color (Table 3). The fact that greater numbers per unit area occur in the larger lakes can be explained by a thicker epilimnetic layer in those lakes. Such an epilimnetic extension is considered to operate as a capacity factor, increasing the volume of suitable environment available for population growth. In the largest lakes the epilimnion extended to about 8–12 m, compared with 3–5 m in the smaller lakes. Also the average number of zooplankters was 2.6 times greater in lakes larger than 25 ha than in those smaller than 25 ha (39 individuals/cm^2 and 15 individuals/cm^2, respectively). These results indicate that the average plankton densities calculated per unit of epilimnion volume were probably

similar in the different size groups of the lakes considered.

The Crustacean Community

The term "limnetic crustacean community" is used here in the broad sense of Dice (1952), Patalas (1954, 1964), Patalas and Patalas (1966), and Pennak (1957). One characteristic of this community is that only a few species are generally abundant, the remainder being scarce. In this study, species more abundant than 10% of the total crustacean number were considered as "dominants" (Patalas 1954, 1964). One to five such dominants per lake were found. A sole dominant, *T. p. mexicanus*, characterized four specific lakes (230, 235, 241, 248), all very small, but relatively deep. A pair of dominant forms distinguished a second group of 13 lakes; the most common combination was one *Diaptomus* species and one cyclopoid species found in all of these 13 lakes. This combination was most frequent in the largest and deepest lakes. A trio of dominants was the most common situation and occurred in lakes of different area and depth. In 18 of the lakes the major forms were usually composed of one cyclopoid, one diaptomid, and one cladoceran species. Communities with four and five dominants were found in 10 lakes of medium size and low to medium depth, but with rather low water transparency. They were composed of two to four cyclopoids, one diaptomid, and one to two cladoceran species. Thus the general scheme of the observed increase in community complexity can be illustrated as follows:

1 cyclopoid
1 cyclopoid + 1 diaptomid
1 cyclopoid + 1 diaptomid + 1 cladoceran
2 cyclopoids + 1 diaptomid + 2 cladocerans

As indicated above only in the more complex communities did cladocerans play a major numerical role. On the other hand, cyclopoids were the most abundant forms in both simple and complex communities. In only two lakes, 224 and 256, was the community simultaneously composed of two dominant diaptomids, *D. minutus* and *D. sicilis*. This congeneric occurrence is explainable upon the basis that whereas *D. minutus* usually occupies the upper layers of water, *D. sicilis* is known to prefer the deeper ones in some lakes (Rigler and Langford 1967; Carter 1969; Patalas 1969).

To indicate the general pattern of the 45 ELA lake communities a schematic diagram is presented in Fig. 4. Four types of communities, based on the dominants and the presence of some other indicator species, can be distinguished. Each of these four types is characteristic of a group of lakes of specific area and depth:

Type I — This community is characterized by the dominance of *C. b. thomasi* and *D. minutus*, and the presence of *L. macrurus* or *S. calanoides*, or both. Usually associated with this type is a high number of species. Representative communities of this category were found in three large lakes (161, 254, 464) ranging from 389 to 1007 ha in area and from 30 to 117 m in maximum depth with high water transparency.

Type II — This community has the same two dominant species, i.e., *C. b. thomasi* and *D. minutus*, but lacks both *Limnocalanus* and *Senecella* species. Fourteen lakes between 6.5 and 200 ha in area and 4.8 and 33 m in maximum depth exhibited this type of community.

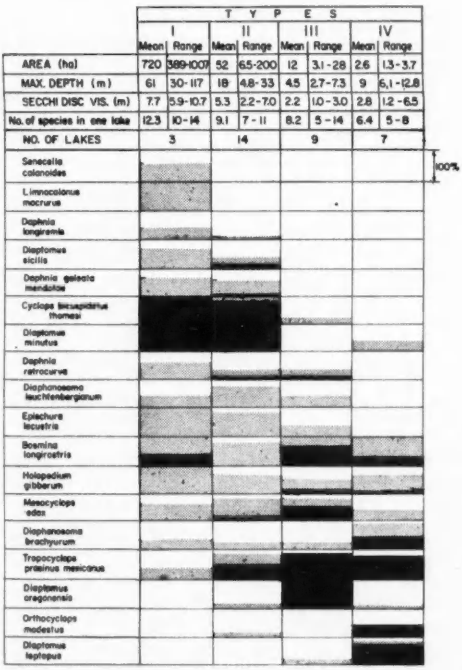

FIG. 4. Four types of crustacean communities in ELA lakes of different size, depth, and water transparency. The height of the block indicates the percentage of lakes of a particular type in which the species was present; the solid part of the block, the percentage of lakes in which the species was dominant.

Type III — This community is characterized by the dominance of *T. p. mexicanus* and *D. oregonensis* in rather small (3.1–28 ha) and shallow (2.7–7.3 m) lakes.

Type IV — This community is dominated by any or all of the following: *T. p. mexicanus*, *D. leptopus*, or *O. modestus*. This arrangement was typical of seven very small lakes (1.3–3.7 ha in area) that were relatively deep (6.1–12.8 m). In contrast to other communities, especially type I, a very low total number of species was found in type IV.

In 11 lakes, communities were found with a structure intermediate between types II and III (e.g., codomination of *C. b. thomasi* and *D. oregonensis*). Also, one lake (132) exhibited a community that was of a character intermediate between types II and IV (domination of *D. minutus* in the presence of *D. leptopus*). In total, then, 74% of the communities can be designated by one of the four particular types, whereas the remaining 26% display intermediate characteristics. This can best be seen in Fig. 5 where particular lakes are plotted on coordinates of area vs. depth, and lakes with the same type of plankton communities are encircled. Almost all communities of the type intermediate between II and III (located in the overlap area) were found in lakes of intermediate depth, mostly between 5 and 10 m.

It should be mentioned again that the pattern of plankton communities discussed above is based mainly on a single series of samples taken in September 1967 or July–August 1968, or both. However, in four lakes (265, 227, 230, and 241) the samples were taken twice, once in September 1967 and once in July 1968. Basically, the same species were found on the two sampling dates; even though the relative abundance of some species in some lakes differed somewhat depending on date (as with *T. p. mexicanus* and *D. leptopus* in lake 230) still the community encountered was the same type. The greatest quantitative differences between September 1967 and July 1968 occurred in lake 227, but even there the community originally described as intermediate between types II and III finally shifted to type II. Thus the relative stability of the community patterns suggests that even a single series of samples taken at a comparable time can provide a representative structural picture. More detailed data on the seasonal changes of the zooplankton communities in two of the lakes are included in the paper by Schindler and Novén (1971).

Several other methods exist for comparing plankton communities amongst themselves (Whit-

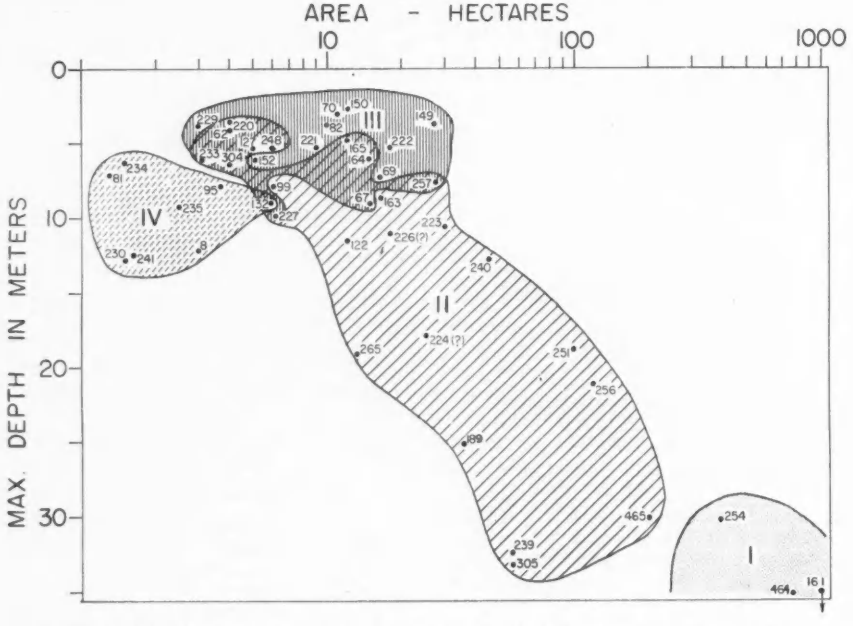

FIG. 5. Morphometric characteristics of lakes with different types of communities.

taker and Fairbanks 1958). One of the simplest is to employ the coefficient of community originally used by Jaccard (1932), which measures the percentage of species common to two communities:

$$CC = \frac{100 \cdot c}{a+b-c}$$

in which a = the number of species in the first community; b = the number of species in the second community; c = the number of species common to both communities. The coefficient equals 100 when two communities are composed of identical species; it equals 0 when two communities have entirely different species (i.e., display no species common to both). Unlike the system described above, the Jaccard community coefficient provides a measure of similarity in species composition, regardless of numerical importance. In Table 4 a matrix of coefficients is presented and lakes with both the most similar and the most dissimilar communities are specifically underlined. Almost all pairs of lakes displaying higher coefficients (>75%) had similar area, depth, and Secchi disc transparency (Table 5). In addition they belonged to the same community type, as previously described. On the other hand, pairs of lakes with lower coefficients (<8%) usually differed in size and depth, and always belonged to different community types or to difficult-to-define mixed types.

In situations where two lakes of different size and depth were in close proximity and were interconnected with each other, no similarity in their plankton community pattern was observed. Such lake pairs as 161 and 162 (CC 8%), 95 and 464 (CC 6%), 305 and 227 (CC 43%), 254 and 152 (CC 31%) provide good examples. On the other hand, lakes 67, 164, and 222, which had not only the most similar plankton communities (see Table 5) but also very similar morphometry, are scattered. Thus within the ELA, it appears that lake area and depth are more significant than location.

To determine the average similarity value of a particular lake with all others in ELA, the sum of all related coefficients was divided by the total number of lakes ($\bar{x}$ in Table 4). On this basis two groups of lakes were distinguished: (1) those whose communities have the highest similarity with most of other lake communities ($\bar{x} > 40$) and thus are most representative for the lake region under study (lakes 67, 163, 164, 189, 221, 222, 223, 240, and 251); (2) those whose communities differ maximally from the rest of lake communities ($\bar{x} < 25$) being least representative of the area (lakes 8, 81, 95, 162, and 241).

Discussion

The general purpose of the present study was to contribute to background knowledge of ELA. Attempts were made to answer several questions: To what degree are ELA lakes representative of larger geographic areas? How uniform are zooplankton populations in the area? Which of the ELA lakes are the most and least representative of the region in terms of zooplankton?

Not all questions can be answered satisfactorily on the basis of the present data, but certain preliminary conclusions can be drawn, which together with other physical, chemical, and biological data, provide a more complete picture of the area.

Some interesting conclusions result when one compares Rigler and Langford's (1967) data on the distribution of calanoid copepods in 100 southern Ontario lakes with the results of the present study (see Table 6). Disregarding the four rare diaptomid species, *D. reighardi*, *D. sanguineus*, *D. birgei*, and *D. ashlandi*, data for the southern Ontario region were strikingly similar to ELA in the percentage occurrence of the remaining most common species. This remarkable coincidence of species composition and frequency of their occurrence in the two lake groups more than 1000 miles apart may suggest that both areas must belong to the same faunistic region. A further comparison is provided by Robertson's data (1966) on the distribution of calanoid copepods in the Great Lakes. With the exception of *Diaptomus leptopus*, a form typical of small lakes, all calanoids found in ELA lakes are present in most of the Great Lakes. The dominant species in the summer plankton of Lake Ontario (Patalas 1969) were *C. b. thomasi*, *B. longirostris*, *D. retrocurva*, and *T. p. mexicanus;* all of them are common and frequently dominant forms in ELA lakes. In one of the largest and deepest ELA lakes, lake 464, 13 species were found that also occur in Lake Ontario. Comparison of August samples from both lakes gave rise to a relatively high coefficient of community of 58%.

A study of *Daphnia* species also indicates certain similarities between the lakes of southeastern Ontario and ELA. To facilitate description of *Daphnia* species distribution in this portion of the North American continent, Brooks (1957) distinguished two zoogeographical areas: zone C, a belt extending from Lake Winnipeg northwest to Great Bear Lake; and zone D, covering the Laurentian Great Lakes area. According to Brooks, *D. retrocurva* and *D. g. mendotae* are common to both zones C and D; however *Daphnia catawba* is limited to zone D. ELA lakes are situated between these two zones and the common occurrence of

TABLE 4. Matrix of the community coefficients (after Jaccard 1932) (the % of common species in a pair of lakes) $CC = \frac{100}{a+b} > 75$ a
are marked with a cross (+), the lowest ones ($\bar{x} < 25$) with a dash (–).

8	67	69	70	81	82	95	99	122	127	132	149	150	152	161	162	163	164	165	189	220	221	222	223	22
·	27	18	37	22	18	25	25	18	28	40	17	11	20	15	13	25	33	27	15	17	19	25	25	3
	·	42	36	25	54	27	36	22	30	50	38	40	46	19	18	46	82	64	46	50	53	90	58	5
		·	40	8	33	18	29	14	33	31	42	44	50	20	33	64	36	54	38	42	47	38	50	3
			·	25	55	37	14	8	25	36	50	37	44	7	11	23	42	36	33	25	25	33	33	2
				·	27	37	14	8	0	25	15	22	18	14	0	7	13	15	14	15	27	23	14	1
					·	30	20	7	20	31	70	44	50	20	9	20	58	55	29	21	47	64	29	1
						·	7	8	13	40	17	25	20	7	13	15	33	17	15	17	19	25	15	
							·	38	40	46	27	25	31	43	40	54	40	36	54	46	41	33	43	4
								·	20	31	13	18	15	38	35	50	27	21	50	42	29	20	38	3
									·	44	30	13	37	8	60	27	25	44	27	18	29	27	27	2
										·	38	27	46	27	18	46	23	50	46	38	53	46	46	4
											·	40	78	12	18	19	43	64	36	29	64	46	36	1
												·	50	15	28	25	33	40	36	55	36	36	50	2
													·	13	22	31	20	60	31	33	50	42	42	2
														·	8	43	24	19	43	36	26	25	33	3
															·	40	15	30	40	30	29	17	27	2
																·	50	46	54	46	50	43	54	6
																	·	67	50	43	47	91	62	3
																		·	46	38	53	73	36	4
																			·	58	60	43	54	6
																				·	44	27	90	3
																					·	60	41	5
																						·	43	4
																							·	4
																								3
																								5
																								·

$= \frac{100}{a+b}$ 75 are marked with a solid line; CC < 10 are marked with a broken line. The highest average community coefficients ($\bar{x} > 40$)

223	227	229	230	233	234	235	239	240	241	248	251	254	256	257	265	304	305	464	465	Lake no.	$\bar{x}$
25	33	20	8	44	30	30	27	30	25	25	27	19	17	22	20	30	27	20	27	8	24–
58	54	46	42	70	54	54	50	54	27	73	64	53	38	50	45	70	50	30	50	67	47+
50	36	67	23	46	23	23	31	33	18	29	22	29	31	27	50	23	22	31	42	69	34
33	21	44	40	40	27	27	15	27	22	23	25	18	15	33	18	40	15	19	25	70	28
14	13	8	55	17	55	55	15	17	57	33	25	18	7	20	8	27	25	12	7	81	20–
29	12	36	60	46	46	46	21	25	30	38	42	29	21	27	15	60	31	24	21	82	33
15	7	20	44	18	44	44	8	18	67	36	27	19	8	22	20	30	17	6	17	95	22–
43	40	31	13	29	29	29	46	64	15	33	46	41	27	23	42	29	46	44	27	99	34
38	36	25	7	14	14	14	42	46	8	20	31	38	21	27	50	23	42	40	31	122	26
27	25	22	9	33	20	20	30	33	13	27	30	20	8	11	37	33	18	21	44	127	25
46	43	14	31	42	55	55	50	55	27	58	50	53	20	25	46	55	38	38	50	132	40
36	18	33	31	42	31	31	29	31	17	36	38	22	20	36	23	42	20	38	38	149	33
50	23	50	44	44	30	30	27	44	25	25	27	27	17	22	33	30	27	20	17	150	31
42	29	40	36	50	36	36	33	36	20	42	46	31	14	30	27	36	23	33	46	152	35
33	31	21	13	20	20	20	36	50	7	24	36	50	36	23	31	29	46	53	19	161	26
27	25	22	9	20	20	20	30	33	13	17	18	20	8	0	50	20	18	21	30	162	22–
54	64	55	13	38	50	50	46	64	15	43	46	50	36	33	70	38	46	44	58	163	42+
62	38	50	36	46	50	50	33	58	23	62	67	56	43	55	38	58	54	33	43	164	45+
36	43	33	31	70	42	42	38	42	17	36	38	35	20	25	46	42	29	29	50	165	40
54	62	42	29	38	29	29	46	64	15	43	46	50	27	23	70	38	46	53	58	189	41+
90	33	46	31	31	21	21	38	55	17	27	38	35	50	36	46	31	38	29	29	220	36
41	56	40	38	29	38	38	44	47	19	41	44	40	21	25	50	47	44	50	53	221	41+
43	40	42	38	50	50	50	36	50	25	67	58	50	36	46	42	64	46	22	46	222	43+
·	40	55	29	38	29	29	46	64	15	33	46	41	58	46	42	38	46	44	36	223	41+
	38	38	19	19	12	12	33	36	7	17	25	25	67	42	29	27	43	50	25	224	30
	50	31	20	50	38	38	46	64	25	54	36	50	36	23	55	50	58	44	46	226	40
	·	29	19	36	27	27	54	46	7	40	33	39	25	21	50	36	43	41	43	227	35
		·	25	50	25	25	25	36	20	31	33	40	33	44	40	25	33	25	33	229	34
			·	33	60	60	13	23	44	38	31	22	21	27	15	46	21	10	13	230	29
				·	46	46	31	33	8	50	42	38	21	27	36	46	31	24	42	233	35
					·	100	31	46	44	64	55	38	21	27	25	60	55	24	31	234	38
						·	31	46	44	64	55	38	21	27	25	60	55	24	31	235	38
							·	89	8	36	38	35	29	25	46	42	50	47	38	239	36
								·	18	50	70	57	31	40	50	60	70	50	31	240	45+
									·	36	27	19	8	22	20	18	17	6	17	241	23–
										·	73	50	27	23	42	50	46	35	58	248	40
											·	53	38	50	33	70	64	47	50	251	43+
												·	35	33	40	47	53	50	44	254	37
													·	50	14	21	50	47	13	256	27
														·	18	40	50	27	25	257	30
															·	36	33	33	60	265	40
																·	55	40	42	304	39
																	·	57	29	305	39
																		·	38	464	33
																			·	465	36

TABLE 5. Pairs of ELA lakes with the most and least similar communities.

Lake characteristics					
Area (*ha*)	Depth (*m*)	Secchi depth visibility (*m*)	Lake	Type of community	Coefficient of community
17.5	5.4	2.2	222	III	91
15.3	6.6	3.7	164	II/III	90
15.1	10.8	3.1	67	II/III	82
1.5	6.1	1.2	234	IV	78
2.8	8.2	1.2	235	IV	
56.1	30.4	4.2	239	II	89
44.1	13.1	4.1	240	II	
28.0	4.2	2.5	149	III	78
5.3	6.1	2.5	152	III	
4.2	3.3	3.3	220	II/III	90
30.2	11.2	4.0	223	II	
3.7	7.6	1.3	95	IV	6
770	37	6.4	464	I	
1007	>117	10.7	161	I	8
4.2	3.8	2.7	162	II/III	8
120	22.4	8.8	256	II	7
1.3	7.0	2.0	81	IV	0
4.7	5.2	3.1	127	II/III	0
4.2	3.8	2.7	162	II/III	0
28.2	7.6	3.5	257	II/III	

D. retrocurva and *D. g. mendotae* in these lakes would confirm Brooks' suggestion about the continuous distribution of these species along the belt of glacial lakes. The presence of *D. catawba* in ELA lakes seems to indicate that this region is a westward extension of Brooks' zone D — Laurentian Great Lakes area.

In attempting to discover the degree of uniformity of ELA lakes, special attention has been placed on the geographic distribution of species within the area. Most species displayed a regular non-contagious distribution, i.e., no particular species were found only in one drainage system or only in lakes situated closely together. However, as previously indicated, similar species groups dominated lakes of the same physical character. On this basis, it would seem fair to conclude that ELA lakes are uniform in the zoogeographic sense and that it is mainly the morphology of a lake that determines its plankton community.

As has been demonstrated, four different types of communities were found, each associated with

TABLE 6. Percentage of lakes of southern Ontario (after Rigler and Langford 1967) and of ELA lakes in which each particular species of calanoids was found.

Species	Southern Ontario (%)	ELA (%)
Diaptomus minutus	70	73
D. oregonensis	69	40
D. sicilis	9	13
D. reighardi	4	0
D. sanguineus	2	0
D. birgei	2	0
D. ashlandi	1	0
Epischura lacustris	49	49
Limnocalanus macrurus	11	6
Senecella calanoides	5	4

a defined type of environment. If we can accept this fact as ample evidence of the relation between community and environment, it would be reasonable to assume the validity of the reverse situation, i.e., through the determination of the planktonic community within a lake, one could make inferences about its environment. At the same time, one would expect that similar lakes with similar communities would respond in a similar way to experimentally induced changes, a prerequisite condition for any experimentation. For this reason, these planktonic communities were analyzed on the basis of their similarity. The predictive values for pairs or groups of lakes that will probably respond in a similar manner to induced changes, as well as of lakes that are rather unlikely to respond similarly, are given. Again, Table 5 indicates two groups of lakes, those most and least representative of the considered area.

Although the generalization that similar environments produce similar communities is usually accepted, it contains inherent difficulties and complexities that demand more critical analysis. For example, complex problems arise when we attempt to define "similar conditions." Several instances are known where a species is considered as characteristic for deep lakes in one region but is typical of shallow lakes in another district. *Diaptomus oregonensis*, defined by Pennak (1957) as a cold-water form occurring only in the northern part of the North American continent in deep lakes, is found according to this definition in many deep southern Ontario lakes (Rigler and Langford 1967) as well as in all St. Lawrence Great Lakes (Robertson 1966). However, it appears to be a characteristic form for small and shallow lakes of ELA, also in shallow Lake Marion in British Columbia (McQueen 1969). *Diaptomus sicilis* was found by Whittaker and Fairbanks (1958) in southeastern Washington as a species typical of saline lakes and ponds whereas in ELA it occurred in large, deep, transparent lakes with very low dissolved solid content. Furthermore, in the northern Colorado Rocky Mountains area *C. b. thomasi* was very common in lakes not deeper than 5 m (Patalas 1964). On the contrary, this species was characteristic of much deeper lakes in ELA. Finally, *Daphnia pulex*, principally a shallow lake and pond dweller (Lilljeborg 1900; Wesenberg-Lund 1939; Brooks 1957; Smyly 1958), seems to be a typical dominant species for deep oligotrophic lakes in northwestern Manitoba (K. Patalas unpublished data). The foregoing examples imply that the ecological characteristics of species and communities can only be considered on a regional basis and that more information is required to clarify the complex interrelations between species and their environment on a broader geographic basis.

Acknowledgments

I am indebted to Mr A. Salki for assistance in preparing the English version of the manuscript. Messrs K. Simpson, D. Mayhood, J. Gray, B. Novén, and P. Campbell were responsible for the considerable effort put into the sample collection. Drs J. R. Vallentyne and D. W. Schindler provided valuable criticism and suggestions that greatly improved the clarity of the manuscript.

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Vertical Distribution and Seasonal Abundance of Zooplankton in Two Shallow Lakes of the Experimental Lakes Area, Northwestern Ontario[1]

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Seasonal variations in the abundance of zooplankton were studied in lakes 122 and 132 for a period of 10 months beginning in mid-May 1968. Seasonal dynamics of various species are discussed in relation to their patterns in the Canadian Shield and in other localities.

Day and night vertical distributions for each lake were sampled on two dates in summer. Three species of rotifers migrated diurnally in lake 122, but no evidence of diurnal movement was found in lake 132. All crustaceans studied in both lakes migrated vertically to some degree, except for nauplius larvae and *Leptodora kindtii*. There was little difference in vertical distribution patterns on the two dates studied.

Average zooplankton biomass in the two lakes was calculated and compared with that found in other studies. Average zooplankton biomass during the ice-free season was 72 and 156 mg/m^3 dry weight for lakes 122 and 132, respectively. Dominant species in both lakes were *Diaptomus minutus*, *Cyclops bicuspidatus thomasi*, *Holopedium gibberum*, and *Bosmina longirostris*. Ecological tolerances for rotifer species agreed well with those found for Swedish waters.

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THE effects of eutrophication upon the zooplankton community, if viewed in the broadest sense, should be twofold: (1) increase in the biomass and production of zooplankton in response to changes in phytoplankton production and phytoplankton species composition; (2) change in the species composition of zooplankton due to changes in food quantity and quality, and possibly in predator faunas.

To interpret these changes we must know natural variation in zooplankton biomass, production, and species composition. Because of the paucity of good life-history data for most species of zooplankton in Canadian Shield lakes, our initial goals have been to study life histories, behavior patterns, and trophic relations for the more important zooplankton species in the Experimental Lakes Area (ELA), so that changes in the zooplankton upon fertilization of a lake might be properly interpreted.

Lakes 122 and 132 were selected for study because they were similar in morphometry to many of the lakes upon which eutrophication experiments were planned (area = 12.2 and 7.2 ha; mean depth = 7.2 and 3.3 m, for lakes 122 and 132, respectively), and because they were close to the temporary camp used in 1968 (Johnson and Vallentyne 1971; also insert map). Further information on morphometry is given by Brunskill and Schindler (1971) and on physical and chemical parameters by Schindler (1971a) and Armstrong and Schindler (1971).

Methods

Vertical series (1-m intervals) of zooplankton samples were taken weekly (monthly in winter) from May 1968 to March 1969 from lakes 122 and 132, using a transparent trap (Schindler 1969). This device proved ideal for vertical distribution studies, since large samples (28.7 liters) could be taken rapidly from discrete depths, and screened through a net fine enough (28 μ) to retain all rotifers and eggs. All sampling was done at one station in each lake (coordinates E6 and F6 on lake 122 and on lake 132; see Brunskill and Schindler (1971), fig. 5 and 6). On several occasions two to four sets of

[1]The tenth in a series of 14 papers on the work of the Fisheries Research Board of Canada, describing background environmental data on the Experimental Lakes Area, northwestern Ontario. For location of numbered lakes see insert map at the back of this issue of the Journal of the Fisheries Research Board of Canada. A key to lake locations is given by Cleugh and Hauser (1971).

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samples were taken over a 24-hr period to determine patterns of diurnal vertical migration. All samples were concentrated to 200 ml and preserved in 4% formaldehyde. At least two aliquots from each sample were counted using an inverted microscope. From 100 to 500 of the more abundant forms were tabulated on each date. Rotifer identifications were made from Ahlstrom (1943), Voigt (1957), and Edmondson (1959). Crustaceans were identified from Edmondson (1959) and confirmed by Dr K. Patalas. It was possible to obtain size ranges and clear photomicrographs of the nauplii of all calanoid species for use in identification. Nauplii of all cyclopoids were counted together, since they could not be distinguished. Copepodid stages of all Copepoda could be distinguished from each other by morphological characteristics and size classes.

Results

Rotifera

Several species of rotifers were numerically important in both intensively studied lakes. In lake 122, *Conochilus unicornis*, *Kellicottia longispina*, *Kellicottia bostoniensis*, *Keratella cochlearis*, *Polyarthra vulgaris*, and *Trichocerca cylindrica* all reached maximum densities in June, and were replaced by *Polyarthra remata* and *Trichocerca rousseletti* later in the summer. *Keratella taurocephala* had two population peaks, one in late June and the second in late August (Fig. 1*a–c*). Other species present in small numbers will not be discussed here.

In lake 132, *K. taurocephala*, *T. rousseletti*, and *C. unicornis* showed seasonal dynamics similar to those of the same species in lake 122, but two of these three species reached maximum densities earlier in lake 132, probably due to warmer temperatures (see Schindler 1971a, fig. 6*g* and *h*). *Keratella cochlearis*, *P. remata*, and *K. bostoniensis* were present only in small numbers in lake 132, whereas *K. longispina* and *P. vulgaris* had seasonal patterns vastly different from lake 122. The former species showed a second population maximum in late summer in lake 132, whereas the latter displayed a single maximum in late summer instead of earlier in the year (Fig. 2*a–b*).

A comparison of the seasonal dynamics of some rotifer species with other situations is possible. Carlin (1943) found *Keratella cochlearis* in the Motala River to exhibit a June maximum similar to that observed in lake 122. He also found a secondary maximum in late summer and a late autumnal increase. Neither was found in lake 122. Davis (1954) found the major population maximum for *K. cochlearis* in Lake Erie to occur in late summer. Schindler (unpublished data) found the species to be most abundant in July in Clear Lake, a Shield lake in eastern Ontario, about 1200 miles to the east.

Kellicottia longispina in lake 122 showed a seasonal pattern similar to those found in the Motala River

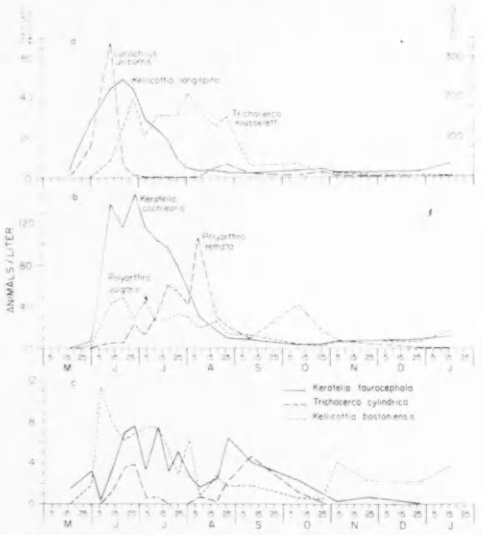

FIG. 1. *a–c*, Seasonal changes in the abundance of dominant rotifer species, 1968, lake 122. Species are indicated in the figures.

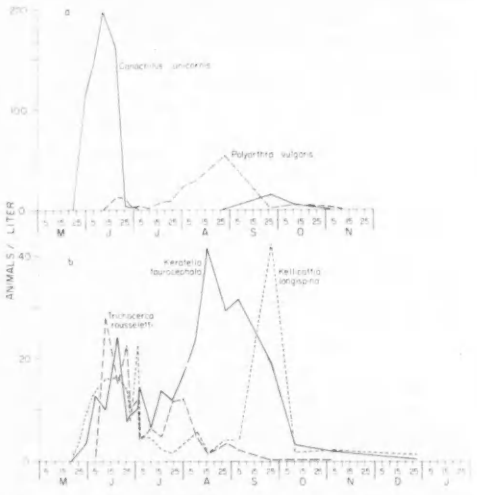

FIG. 2. *a–b*, Seasonal changes in the abundance of dominant rotifer species, 1968, lake 132. Species are indicated in the figures.

and Clear Lake. The greatest abundance in lake 132 occurred several weeks later. *Conochilus unicornis* populations had similar dynamics in all cases. *Polyarthra vulgaris* in lake 132 supported the observation of Hutchinson (1967) by occurring later in the season than other cosmopolitan and perennial species, although its maximum abundance in lake 122 occurred as early as that of any other rotifer, whereas *P. remata* occurred still later in the summer. Carlin (1943) found a similar pattern.

Keratella taurocephala showed the same seasonal pattern in all lakes available for comparison. In lake 132 and in Clear Lake, a small population peak in early June was followed by a major maximum in mid-July. The equivalent two peaks in lake 122 were several weeks later and nearly equal in size. *Kellicottia bostoniensis* had a June–July maximum in both lake 122 and Clear Lake, followed by a second peak in late fall and winter. A general review of rotifer seasonal dynamics is given by Hutchinson (1967).

Some diurnal vertical movement of rotifers was evident in both lakes, although the amplitude was always small. Figures 3 and 4 show typical daylight and nighttime distribution patterns. Maximum concentrations of *K. longispina* in lake 122 were about 1 m higher at night (Fig. 3*a* and *b*) whereas *C. unicornis* formed two nighttime maxima, one about 1 m above the daylight maximum and the other at the water surface. Two daylight maxima of *K. cochlearis*, at 7 and 9 m, appeared to merge at 7 m during the night. Although some slight upward trends were noticed in nighttime samples from lake 132, they are not distinctive enough to be interpreted as evidence for vertical migration (see Fig. 4). The small amplitudes of vertical movement mentioned for the above three species did not occur through zones of great change in their food or temperature regimes (see data of Armstrong and Schindler 1971 and Schindler 1971a). Similar slight diurnal changes have been mentioned previously in the literature, for *C.* cf. *unicornis* in Grosser Plöner See and for *K. cochlearis* in Lake Aoki (see Hutchinson 1967 p. 732). There appears to be no previous evidence for diurnal migration by *K. longispina*.

There appeared to be little, if any, seasonal change in the depth distribution of major rotifer species, although population densities were an order of magnitude lower in late summer (Fig. 3*e* and *f*). The maximum density of total rotifers was always concentrated near the region of maximum phytoplankton abundance (Fig. 5), where a chlorophyll *a* profile is shown along with the vertical distribution of the rotifers.

Some comparisons of ecological tolerances of rotifer species in ELA lakes with those found by other workers are also of interest. Hutchinson (1957 p. 549–551) reviews the subject. For a soft-water area on igneous rock, the investigations of

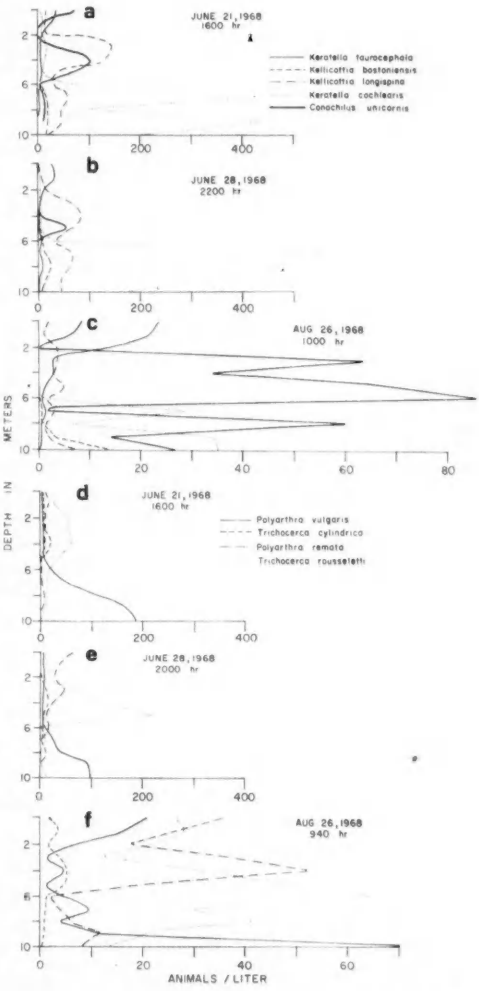

FIG. 3. *a–f*, Diurnal and seasonal changes in the vertical distribution patterns of major rotifer species, 1968, lake 122. Sampling depths, species, and time of sampling are indicated in the figures. Daytime and nighttime patterns depicted are from different dates, so that the maximum amplitudes of diurnal and seasonal movements are illustrated. Diurnal movements were similar on all dates tested.

Pejler (1961, 1962, 1965) on Swedish lakes are the most interesting.

The species *Ploesoma hudsoni*, *Synchaeta grandis*, and *Collotheca libera*, considered by Pejler (1965) to be indicators of oligotrophy, are widespread in ELA, though only the last-named species was recorded from lakes 122 and 132 (Table 1). Pejler (1962, 1965) also observed that *K. longispina*, *K. cochlearis*, and *P. vulgaris* were dominant in most oligotrophic lakes, whereas *Gastropus stylifer*, *Asplanchna priodonta*, *P. remata*, *Conochilus* spp., and *Ascomorpha ovalis* were common. These observations all agree well with our findings for ELA lakes.

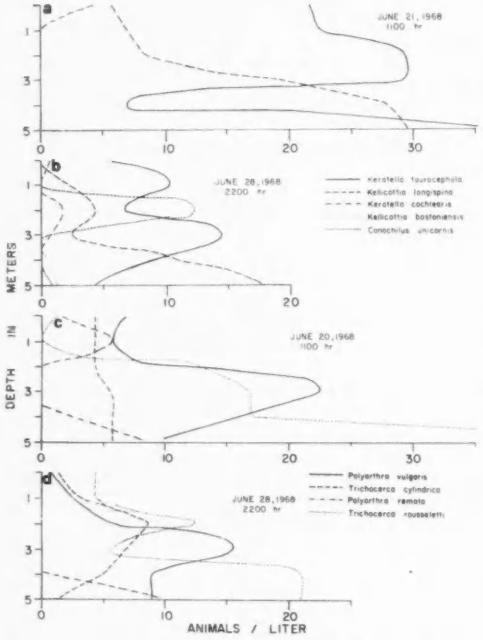

FIG. 4. *a–d*, Diurnal and seasonal changes in the vertical distribution patterns of major rotifer species, 1968, lake 132. Species and time of sampling are indicated in the figures. Panels were chosen as for Fig. 3.

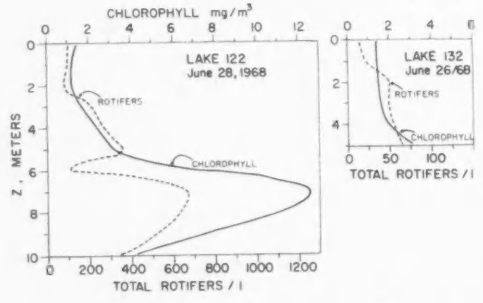

FIG. 5. Typical examples of the distribution of chlorophyll *a* and rotifers with depth, lakes 122 and 132. Patterns were similar throughout the summer.

Of species listed by Pejler (1965) as indicators of eutrophy that we would expect to be absent or sparsely distributed in the oligotrophic ELA lakes, *Brachionus angularis* and *Anuraeopsis fissa* are rare. *Polyarthra euryptera*, *Pompholyx sulcata*, *Trichocerca birostris*, *T. pusilla*, and *K. cochlearis* f. *testa* have not been found in ELA.

A few observations do not agree. *Filinia longiseta* and *T. cylindrica*, both common in ELA, are considered by Pejler to be indicators of eutrophy in Swedish waters.

The genus *Brachionus* is usually considered to be an indicator of alkaline waters. We have found *B. angularis* at *p*H 6.5 in ELA lakes, though in small numbers. *Keratella taurocephala*, common in ELA, is usually considered to be an indicator of dilute or acid waters. The genus *Filinia* is sometimes considered to be limited to alkaline waters, which does not agree with our findings. Hutchinson (1967) and Pennak (1953) discuss the topic.

Table 1 lists all genera found in lakes 122 and 132, plus species identifications where possible. More complete taxonomic information will be published at a later date.

COPEPODA

The calanoid copepod *Diaptomus minutus* outnumbered other crustacean species in both lakes. Maximum reproduction occurred before mid-June in both instances, as found by Davis (1961) for the species in Lake Erie, and by Schindler (unpublished data) in Clear Lake and lake 239. Individuals developed more rapidly in lake 132 than in lake 122, probably because the former was shallower and therefore warmer. Low but sporadic egg production occurred throughout the summer in both lakes, though the mortality was extremely high for late-hatching animals as indicated by the small peaks for nauplii and copepodids in late summer. A similar pattern was found in Clear Lake. Only late copepodids were present by midautumn, and all surviving animals had reached adulthood by freeze-up. Although sampling was not begun

TABLE 1. Pelagic rotifers from lakes 122 and 132.

Lake 122	Lake 132
Keratella cochlearis (Gosse)[a]	*K. cochlearis*
K. taurocephala Myers	*K. taurocephala*
K. cf. *irregularis* (Lauterborn)[b]	*K.* cf. *irregularis*
K. hiemalis Carlin	*K. hiemalis*
Kellicottia longispina (Kellicott)	*K. longispina*
K. bostoniensis (Rousselet)	*K. bostoniensis*
Conochilus unicornis Rousselet	*C. unicornis*
C. cf. *hippocrepis* (Schrank)	*P. vulgaris*
Polyarthra vulgaris Carlin[c]	*P.* cf. *remata*
P. cf. *remata* Skorikov	*S. oblonga*
P. minor Voigt	*T. cylindrica*
Synchaeta oblonga Ehrenberg	*T.* cf. *rousseletti*
Synchaeta sp.	*Trichocerca* sp.
Trichocerca cylindrica (Imhof)	*A. priodonta*
T. cf. *rousseletti* (Voigt)	*F. longiseta*
Trichocerca sp.	*C.* cf. *libera*
Asplanchna priodonta Gosse	*G. stylifer*
Filinia longiseta (Ehrenberg)	*Gastropus* cf. *hyptopus* (Ehrenberg)
Collotheca cf. *libera* (Zacharias)	*A.* cf. *saltans*
Gastropus stylifer Imhof	*Notholca* sp.
Ascomorpha ovalis Carlin	*Lecane* cf. *stichaea* Harring
A. cf. *saltans* Bartsch	*Lecane* cf. *flexilis* (Gosse)
Lecane cf. *ploenensis* (Voigt)[d]	*C. dossuarius*
Conochiloides dossuarius Hudson	*P.* cf. *formosa*
Pseudoploesoma cf. *formosa* (Myers)	*Anuraeopsis fissa* (Gosse)
Lepadella sp.	*Elosa woralli* Lord
Brachionus angularis Gosse	*Trichotria* cf. *tetractis* (Ehrenberg)

[a]Anterior third of ventral surface pustulate on some specimens.
[b]Larger than *K. cochlearis* and similar in many ways to *K. earlinae*.
[c]Some specimens smaller than others and with longer paddles somewhat similar to *P. longiremis*. It is impossible at present to tell whether the two forms are genetically isolated.
[d]Some similarities to *L. stichaea*.

early enough in the spring of 1968 to determine maximum egg numbers in lakes 122 and 132, maximum egg abundance occurred under ice in Clear Lake, in lake 239, and in Lake Erie (Davis 1961). It is likely that a similar pattern appears in lake 132, but no eggs were found on winter animals from lake 122 (Fig. 6*a–b*). Two other species, *Diaptomus leptopus* and *Epischura lacustris* were found in lake 132, though in small numbers. All three species are widespread in the Canadian Shield (Patalas unpublished data; Schindler unpublished data).

Cyclops bicuspidatus thomasi was the prevalent cyclopoid copepod in both lakes. The species was dicyclic in lake 122, with a large hatch of eggs in fall followed by slow maturation under the ice (Fig. 7*a*). No fall-hatched animals in 1967 reached adulthood by spring breakup in 1968, and the small spring pulse of eggs in 1967 was probably caused by a small number of overwintering adults. The early spring copepodid maximum, preceding even the maximum abundance of nauplii, is probably caused by animals that overwintered in or near the bottom, and therefore could not be captured during the winter months. Further evidence is needed. An almost identical picture was found in Clear Lake, eastern Ontario (Schindler unpublished data).

The seasonal cycle of *C. b. thomasi* was completely different in lake 132, with three pulses of egg production in midsummer (Fig. 7*b*). The species has been found to enter a summer diapause stage in Wisconsin and Minnesota lakes (Hutchinson 1967 p. 613), a phenomenon that was not observed in lakes 122 and 132.

Tropocyclops prasinus mexicanus also occurred in lake 132 in moderate numbers (Fig. 8). *Tropocyclops* hatched in May, and the first adults

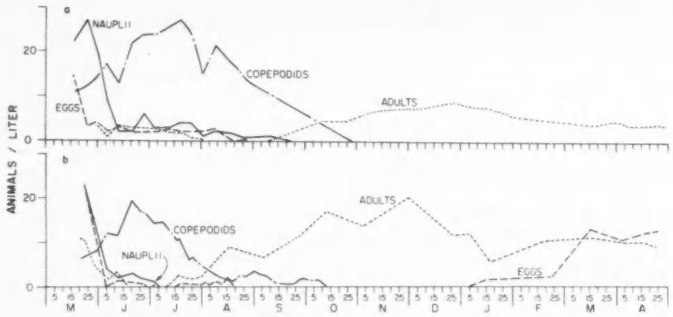

FIG. 6. Seasonal changes in the abundance of *Diaptomus minutus*, 1968–69: *a*, lake 122; *b*, lake 132.

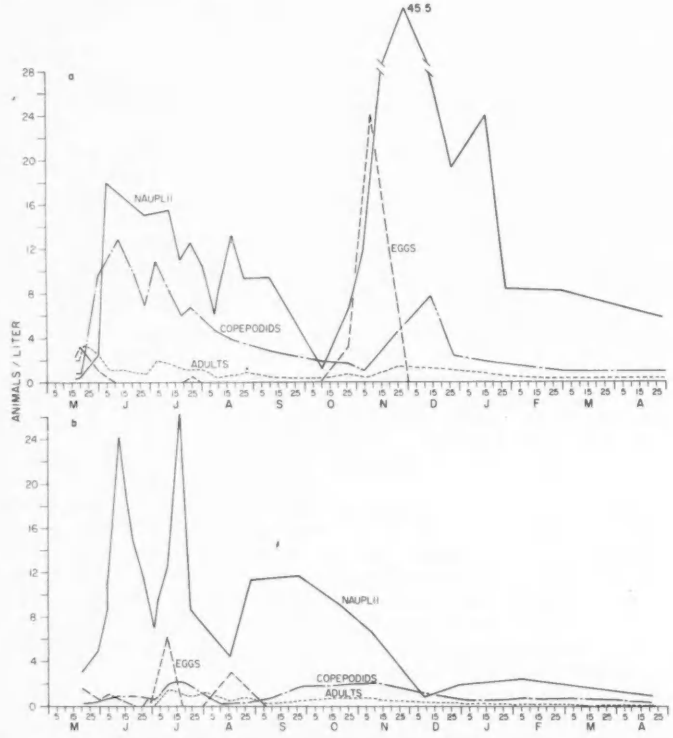

FIG. 7. Seasonal changes in the abundance of *Cyclops bicuspidatus thomasi*, 1968–69: *a*, lake 122; *b*, lake 132. Nauplii of *Tropocyclops prasinus* are included.

appeared in mid-July. These overwintered, developing egg sacs under the ice. Nauplii could not be distinguished from those of *C. b. thomasi* and are included in the figure for the latter species. Too little is known about the seasonal dynamics of this species to say whether the observed pattern is typical. The species is common in the Great Lakes and throughout the Canadian Shield. *Mesocyclops edax* was also found in lake 132, though infrequently. The species was absent from lake 122.

FIG. 8. Seasonal changes in the abundance of *Tropocyclops prasinus mexicanus*, 1968–69, lake 132. Nauplii were included with *Cyclops bicuspidatus thomasi* in Fig. 7*b*.

CLADOCERA

Several species of Cladocera were common, though numerically they seldom dominated the Crustacea of lakes 122 and 132. *Bosmina longirostris* and *Holopedium gibberum* were dicyclic in both lakes, exhibiting spring and late summer or autumn maxima (Fig. 9*a–b*). The same pattern was found in Clear Lake, eastern Ontario. Both species have been found to be monocyclic in some situations and dicyclic in others (Hutchinson 1967; Schindler unpublished data). The latter species is considered to be an indicator of oligotrophic soft waters (Pejler 1965). *Diaphanosoma* was monocyclic in both lakes, reaching highest densities in July and August, then disappearing by midautumn. Such a seasonal cycle appears to be typical (Hutchinson 1967; Schindler unpublished data). *Daphnia galeata mendotae* and *Daphnia longiremis* were present in lake 122, the former reaching a single maximum in late June (Fig. 10*a*). Birge (1898) found *D. galeata* to have both spring and autumn maxima in Lake Mendota. The latter species had a bimodal midsummer maximum in the hypolimnion of the lake, then a second peak under winter ice. This winter maximum is difficult to explain even though egg-bearing animals were present, since hatching under ice should be extremely slow. It is possible that the species concentrated in the shaft of light falling through the sampling hole in the ice, causing overestimates of their abundance, since half an hour often elapsed between cutting a hole in the ice and taking samples. *Daphnia longiremis* is usually regarded as a cold stenotherm, a conclusion supported by the fact that it did not occur above the thermocline in lake 122 (Fig. 11*b*). The record of males in late fall is apparently unusual in North America; a single specimen was used by Brooks (1957) to depict the sex. Ruttner (1930) records male *D. longispina* from Lunzer Untersee. This species and possibly *B. longirostris* appear to be the only cladocerans that overwinter in ELA.

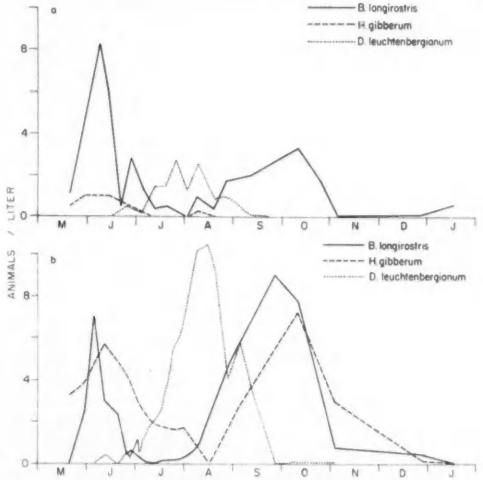

FIG. 9. Seasonal changes in the abundance of *Bosmina longirostris*, *Holopedium gibberum*, and *Diaphanosoma leuchtenbergianum*, 1968–69: *a*, lake 122; *b*, lake 132.

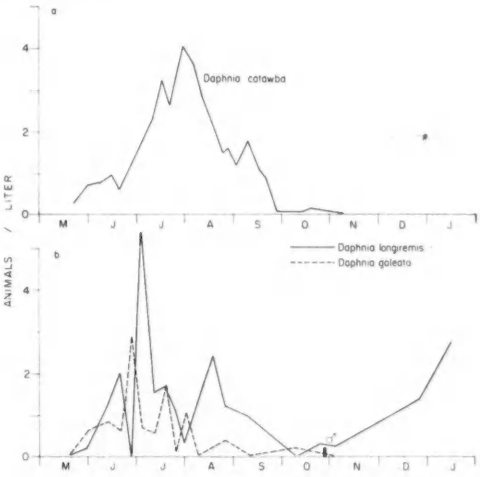

FIG. 10. Seasonal changes in the abundance of *Daphnia* spp., 1968–69: *a*, lake 122; *b*, lake 132.

Neither of the above species occurred in lake 132, where *Daphnia catawba* was the only representative of the genus, again having a single midsummer maximum (see Fig. 10*b*). *Leptodora kindtii* also appeared for a short interval in late June and early July in lake 132, but only in small numbers.

Vertical Migration of Crustacea

Most crustaceans concentrated near the depth of maximum phytoplankton abundance for all or part of the day (Fig. 5, 11, and 12).

In general, small species and stages of Calanoida migrated diurnally less than larger species. Nauplius larvae did not migrate at all in lake 122, the majority remaining at 7 m. The population maximum in lake 132 appeared to shift upward about 1 m during the day. *Diaptomus minutus* copepodids and adults migrated upward about 2 m at night in lake 122, but vertical movement in lake 132 was slight, and possibly downward at night. This species has been found to make slight diurnal migrations wherever found, usually being confined largely to the epilimnion of deeper lakes that it inhabits (Langford 1938; Rigler and Langford 1967; Sandercock 1967; Patalas 1969; Carter 1969). Carter (1969) found the species to be uniformly distributed throughout the water column during spring and fall turnover. A more pronounced diurnal migration was exhibited by *D. leptopus* in lake 132. No cyclopoids were included in vertical distribution studies. Diurnal vertical migrations of *T. prasinus* and *C. b. thomasi* were observed by Patalas (1969) and seasonal distribution patterns of the same species by Carter (1969) in the Great Lakes, with amplitudes of 10–20 m.

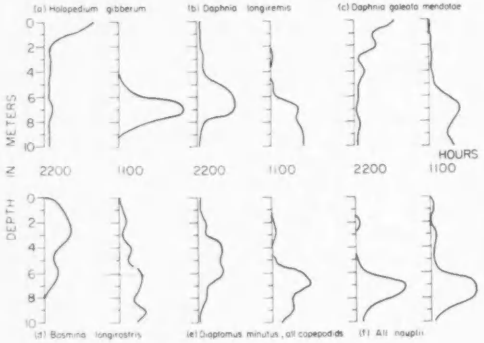

FIG. 11. Diurnal changes in the vertical distribution of crustacean zooplankton, lake 122. Values at each depth are expressed as percent of the total number of animals at all depths. 2200 hr, July 28, 1968; 1100 hr, July 29, 1968.

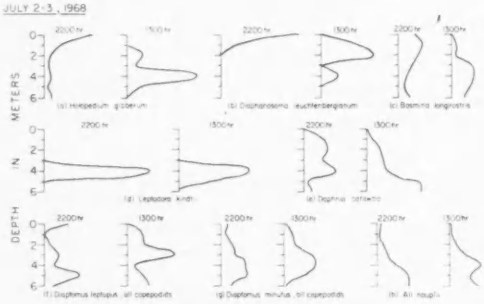

FIG. 12. Diurnal changes in the vertical distribution of crustacean zooplankton, lake 132. Values at each depth are expressed as percent of the total number of animals at all depths.

All herbivorous cladocerans showed some diurnal vertical movement. *Holopedium gibberum* migrated farthest, covering a distance of several meters in order to swarm at the lake surface at night. *Bosmina longirostris* and *Diaphanosoma leuchtenbergianum* showed movements of a few meters. *Diaphanosoma brachyurum* from lake 122 was not present in sufficient numbers to analyze on the date of sampling. *Daphnia longiremis* confined its migration in lake 122 to the hypolimnion, whereas *D. g. mendotae* migrated through the thermocline. *Daphnia catawba* in lake 132 showed a migration of small amplitude (see also Tappa 1965). *Leptodora kindtii* in lake 132 did not migrate at all, presumably to remain at the depth where prey were most abundant, 4 m.

A late-summer analysis showed diurnal migration patterns very similar in all instances to those found in July. It is therefore not shown here.

Zooplankton Biomass

Table 2 lists all crustaceans identified from the limnetic areas of both lakes. It was not possible to calculate seasonal zooplankton production for the two lakes, since spring sampling was not begun early enough to allow determinations of the numbers and durations of early instars. A comparison of zooplankton biomass with that of other lakes is, however, of some interest, though the shortcomings of biomass calculations alone permit only the grossest comparisons.

Dry weights for *C. b. thomasi*, *D. minutus*, *H. gibberum*, *B. longirostris*, *Diaphanosoma* spp., and *Daphnia* spp., were taken from the Clear Lake study mentioned earlier and applied to lakes 122 and 132. Rotifer volumes were calculated by assuming them to be of simple geometric shapes, usually

TABLE 2. Crustacean identifications from lakes 122 and 132.

Lake 122	Lake 132
Copepoda	
Diaptomus minutus Lilljeborg	*D. minutus*
Cyclops bicuspidatus thomasi Forbes	*C. b. thomasi*
	D. leptopus Forbes
	Epischura lacustris Forbes
	Tropocyclops prasinus mexicanus Kiefer
	Mesocyclops edax Forbes
Cladocera	
Daphnia longiremis Sars	*Daphnia catawba* Coker
Daphnia galeata mendotae Birge	*H. gibberum*
Holopedium gibberum Zaddoch	*B. longirostris*
Bosmina longirostris (O. F. Müller)	*D. leuchtenbergianum*
Diaphanosoma brachyurum (Liéven)	*Leptodora kindtii* Focke
Diaphanosoma leuchtenbergianum Fischer	*Polyphemus pediculus* (Linné)
Sida crystallina (O. F. Müller)	*S. crystallina*
	Chydorus sphaericus (O. F. Müller)
	Alona intermedia Sars
	Acroperus harpae Baird
	Monospilus sp.

cylinders or ellipsoids. The dry weight of rotifers was assumed to be 5% of the wet weight, assuming a density of 1.00.

Comparisons with other studies proved most difficult, since some authors have presented their data as zooplankton volumes or wet weights. Conversions of these data were made assuming factors of 6% (dry weight/wet weight) and 1.00 (live density). Different sampling methods were used, which were undoubtedly of different efficiency (Patalas 1954; Schindler 1969). Seasons of sampling did not correspond in all instances, though only May through October data were used in comparisons when these data were given (Table 3).

Three rough groupings are discernable. Lago Maggiore, Lake Baikal, and Lake Smolak all have very low zooplankton biomass, 24–51 mg/m^3 dry weight. Lake Erken, Canyon Ferry Reservoir, and Severson Lake, all eutrophic, have biomasses over an order of magnitude higher. Lakes 122 and 132 fall in the intermediate group, consisting chiefly of ponds and shallow lakes or other lakes in the Shield.[2] Where data are given, larger lakes appear to be dominated by Copepoda, and smaller lakes by Cladocera. It is tempting to attribute the low percentage of rotifers in Clear and Severson lakes to the fact that a no. 20 (70 μ) townet was used, which would allow some specimens to pass through the mesh, but Ravera (1969) records a high percentage of rotifers from Lago Maggiore using a townet. His study must be given very high consideration since dry biomass figures for all groups were determined by actually drying and weighing samples. Table 4 lists weights used in conversions of all species numbers to dry biomass in lakes 122 and 132.

[2]Excluding very humic lakes, which appear to have disproportionately large zooplankton standing crops.

Discussion

Although most of the species common in lakes 122 and 132 are widespread in ELA, interpretation of changes in species composition and seasonal dynamics upon fertilization will probably prove extremely difficult due to great natural variation. As mentioned above, most of the cladoceran species found in lake 122 and 132 have been found to be monocyclic by some authors and dicyclic by others. Another highly variable species is the copepod *D. minutus*. Females of this species carried no eggs under winter ice in lake 122, whereas in lake 132 eggs were present by early January and abundant by March (Fig. 6*a–b*). In other lakes (Clear Lake, lake 227), hatching has taken place under ice, and third or fourth nauplius stages are present by ice-out in the spring (Schindler 1971b). Carter (1969) presents data for adults of this species that suggest that the species may be dicyclic or at least bimodal in Parry Sound, whereas Langford's (1938) results for Lake Nipissing show only one peak of adults in the summer of 1934, and no distinct maximum in 1935. The differences in seasonal

TABLE 3. A comparison of average zooplankton biomass from lakes 122 and 132 with that found in other lakes. May through October data were used if given.

Lake	Country	Source	Crustacea (mg/m^3 dry wt)	Total zooplankton (mg/m^3 dry wt)	% Crustacea		% total zooplankton			Method of collection	Lake type
					Copepoda	Cladocera	Copepoda	Cladocera	Rotifera		
Upinek	Poland	Patalas & Patalas 1968	268[a]	–	–	–	–	–	–	5-liter trap	Pond/eutr.
Piecek	"	"	147[a]	–	–	–	–	–	–	–	Dyst/eutr.
Arklickie	"	"	144[a]	–	–	–	–	–	–	–	Pondlike
Lemiet	"	"	123[a]	–	–	–	–	–	–	–	Eutrophic
Zywy	"	"	82[a]	–	–	–	–	–	–	–	Eutrophic
Smolak	"	"	51[a]	–	–	–	–	–	–	–	Dystrophic
Maggiore (Bay of Ispra)	Italy	Ravera 1969	27	30	76	24	68	22	10	Townet	Oligotrophic
Erken	Sweden	Nauwerck 1963	540[a]	540	80	20	80	20	0	Water bottle	Eutrophic
Canyon Ferry Reservoir	USA	Wright 1958	–	402	–	–	–	–	–	Kemmerer bottle	Eutrophic
Severson	USA	Schindler (unpubl.)	1099	1126[b]	42	58	42	56	2	Clarke–Bumpus	Polytrophic
Baikal	USSR	Kozhov 1963	–	24–48	–	–	–	–	–	–	Oligotrophic
Clear	Canada	Schindler (unpubl.)	142	145[b]	39	61	38	60	2	Townet	Oligo/meso
122	Canada	Present study	72	81[b]	61	39	61	28	12	29-liter trap	Oligo/meso
132	Canada	Present study	156	169[b]	37	63	34	58	12	29-liter trap	Oligo/meso

[a]Converted to dry weight by assuming dry weight = 0.06 wet weight.

[b]Rotifers were converted to dry weight by assuming dry weight = 0.05 wet weight, except for *Asplanchna* where dry weight/wet weight was assumed to equal 0.01.

TABLE 4. Weights used in conversions to dry biomass for lakes 122 and 132.

		Dry wt, μg/animal
Diaptomus minutus	adults	4.50
	copepodids	1.60
	nauplii	0.40
	eggs	0.07
Cyclops bicuspidatus thomasi	adults	4.05
	copepodids	1.52
	nauplii (including *T. prasinus*)	0.34
	eggs	0.06
Daphnia longiremis		4.8[a]
D. galeata		10.2[a]
D. catawba		5.3
Diaphanosoma spp.		6.1
H. gibberum		20.0
B. longirostris		2.0
		mm³, live volume
Keratella cochlearis		0.0007
K. taurocephala		0.0012
Kellicottia longispina		0.0018
K. bostoniensis		0.0009
Polyarthra vulgaris		0.0014
P. remata		0.0007
Conochilus unicornis		0.004 (colony)
Trichocerca cylindrica		0.0001
T. rousseletti		0.0001

Other rotifer volumes were taken from Nauwerck (1963)

[a]Taken from *Daphnia* length–weight curve of Schindler (1968).

dynamics of this species between lakes that we have studied appear to bear little relation to either phytoplankton abundance or temperature, and the matter needs further investigation. Even less is known of natural seasonal variation in other species of copepods, or in rotifer species in the Canadian Shield. Further information on natural variation in dynamics and species composition is needed before changes in zooplankton accompanying fertilization experiments may be accurately interpreted.

Acknowledgments

Dr K. Patalas kindly confirmed many of the crustacean identifications and provided valuable criticism of the manuscript. Dr J. Gilbert identified *Asplanchna priodonta*. Mr F. A. J. Armstrong furnished the chlorophyll *a* data shown in Fig. 5. Dr A. Nauwerck identified some of the rotifer species and provided valuable discussion of their variation.

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Zoobenthos of Fifteen Lakes in the Experimental Lakes Area, Northwestern Ontario[1]

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The composition of the profundal and sublittoral zoobenthos of 15 lakes in northwestern Ontario was closely related to morphometric features of the individual lakes. The amphipod *Pontoporeia affinis* Lind., and the sphaeriid *Pisidium conventus* Clessin, were the dominant species in the larger deeper lakes whereas species of Chironomidae and Chaoborinae were the dominant forms in all lakes with mean depths of less than 10 m. Dissolved oxygen concentration and temperature of the bottom water, two characteristics that are largely a function of lake morphometry, are probably the primary factors limiting the distribution of individual species.

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THE objectives of this investigation were to define the main features of the benthic communities in lakes within the Experimental Lakes Area (ELA) and to correlate these features with environmental parameters. The study was restricted to the sublittoral and profundal zones of 15 lakes in ELA. These lakes represent a variety of morphometric types with maximum depths ranging from 2.5 to about 117 m and surface areas from about 1.3 to 1008 ha. A summary of the relevant physical and chemical characteristics of the lakes in the area is given by Armstrong and Schindler (1971), Brunskill et al. (1971), Brunskill and Schindler (1971), and Schindler (1971).

Previous information on the benthos of Precambrian Shield lakes in Canada is, for various reasons, not directly comparable with what is being attempted here. Most previous studies have been of much larger lakes, usually on the southern boundary of the Shield. Examples include Rawson (1953, 1960), Oliver (1960, 1964), and Slack (1967). Miller (1941) gives a detailed analysis of the chironomids of a small Precambrian Shield lake but other components of the fauna were not treated.

Methods

A total of 121 samples was collected with a 15 × 15 × 23-cm tall Ekman dredge equipped with a No. 30 brass wire mesh (apertures approximately 60 μ square) across the top. All samples were taken at least 10 m from shore and in most lakes a total of 10 samples from two or three transects were analyzed. Sampling was conducted during the period from May 1–14, 1969, i.e., within 3 weeks of the disappearance of ice cover. Only about three of the common species were beginning to emerge by this time; consequently the problem of interpreting species abundance was only moderately complicated by the emergence of insects. In this series of samples the screen-equipped dredge was always lowered slowly so as to minimize pressure buildup and the associated blowout of surface sediments. The accessory screen used with the Ekman dredge was a necessity because most of the lake sediments encountered are so soft that it is impossible for the dredge operator to detect when the dredge reaches the sediment surface. Test samples with an unmodified Ekman dredge often yielded no organisms because the sampler penetrated beneath the surface layer. A multiple core sampler has since been developed for use in these very soft sediments (Hamilton et al. 1970).

All the samples analyzed were sieved through nylon mesh nets (apertures 400 μ sq) except those from lakes 81, 303, and 304 where the sediments were extremely difficult to sieve and a larger mesh (apertures 600 μ sq) was required to reduce the sieve residue to about 200 cc. The residues were preserved in 10% formalin. Later the contents were emptied into a large half black and half white pan and forceps were used to separate the organisms from the residue. Samples containing large quantities of residue (more than about 100 cc) were first stained with rhodamine B and then examined with longwave ultraviolet light (Hamilton 1969). Organisms were preserved in 70–75% ethanol. Identification,

[1]The eleventh in a series of 14 papers on the work of the Fisheries Research Board of Canada, describing background environmental data on the Experimental Lakes Area, northwestern Ontario. For location of numbered lakes see insert map at the back of this issue of the Journal of the Fisheries Research Board of Canada. A key to lake locations is given by Cleugh and Hauser (1971).

Printed in Canada (J1843)

counting, and enumeration were done with the aid of a dissecting microscope. When necessary, specimens were mounted on slides as outlined by Sæther (1969) and identified using a compound microscope. All major components of the fauna except the Oligochaeta were identified at least to genus and usually to species. The major groups are classified according to Bousfield (1958), Herrington (1962), Hamilton et al. (MS 1969), and Sæther (1970).

Results and Discussion

The benthic faunas of lakes in ELA proved to be very diverse. Not surprisingly the major physical and chemical features that have given rise to this diversity appear to be depth, temperature, and the level of dissolved oxygen.

For the purposes of discussion two relatively stable physical parameters, mean depth and surface area, were used to divide the lakes into six general categories. This somewhat arbitrary classification is outlined graphically in Fig. 1. The diagnostic physical and biological features of the lakes in each of the categories may be summarized as follows:

(A) Rather small (9.93 ha) shallow (z_m = 2.5 m) lakes with a low relative depth[2] (z_r = 0.70). Stratification[3] type III. Benthos primarily Diptera. Dominants[4] all Chironomidae. One lake investigated. (B) Very small (1.3–1.67 ha) relatively deep (z_m = 7.0–13.6 m) lakes with high relative depths (z_r = 5.44–9.33). Stratification type I, including one meromictic lake. Benthos primarily Diptera. Dominants all Chaoborinae and Chironomidae. Three lakes investigated. (C) Small (3.62–7.17 ha) shallow (z_m = 6.7–10.0 m) lakes with typical relative depths (z_r = 2.78–3.96). Stratification type I, II, or III. Benthos primarily Diptera. Dominants all Chaoborinae and Chironomidae. Four lakes investigated. (D) Lakes of intermediate size (12.2–44.1 ha) and depth (z_m = 12.8–13.8 m) with typical relative depths (z_r = 1.75–3.25). Stratification type I or II. Benthos primarily Diptera. Dominants all Chaoborinae and Chironomidae. Three lakes investigated. (E) Rather large (52.0–181 ha) deep (z_m = 30–32.7 m) lakes with typical relative depths (z_r = 1.98–4.02). Stratification type I or II. Benthos primarily Amphipoda and Sphaeriidae. Dominants all Amphipoda and Sphaeriidae. Three lakes investigated. (F) Large (~1008 ha) very deep (z_m = 117 m) lakes with a typical relative depth (z_r = 3.27). Stratification type I. Benthos primarily Amphipoda and Sphaeriidae. Dominants all Amphipoda and Sphaeriidae. One lake investigated.

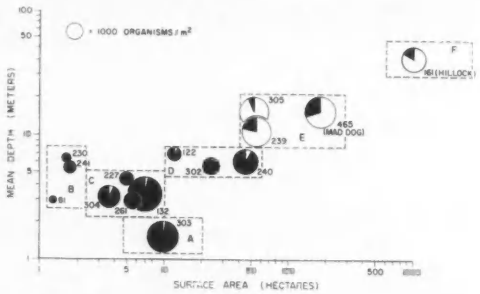

FIG. 1. Importance of mean depth and surface area to the distribution of invertebrates in ELA lakes. Rectangles indicate "approximate" boundaries of categories treated in text. The areas of the circles are proportional to the estimated standing crop of benthic macroinvertebrates and the darkened portions correspond to the percentage Diptera. Locations of lakes are indicated on ELA insert map.

A more detailed list of the physical and chemical features of these ELA lakes is presented in Table 1. Within categories, lakes with lower relative depths generally have higher bottom temperatures. The lakes in category B are exceptions probably because the relative depths of all of them are high. Partly as a consequence of this the thermal and chemical stratification is strong and little hypolimnetic warming occurs in any of them. Lake categories E and F include only those lakes that have strong thermal stratification, yet because of the large volume of the hypolimnion they do not suffer severe oxygen depletion.

Some of the influence of these physical and chemical features on the bottom fauna is summarized in Table 2. All of the smaller lakes, whether thermally stratified or not, had a benthic macroinvertebrate fauna consisting overwhelmingly of Diptera. Numerically they made up from 85.7 to 99.2% of the fauna in categories A–D. The larger, thermally stratified, and well-oxygenated lakes in categories E and F are in sharp contrast to this. In them, Diptera made up only 11.2–30.1% of the fauna compared with percentages of 31.4–68.5 and 15.7–27.1 for the Amphipoda and Sphaeriidae respectively. In addition the dominant

[2]Following Hutchinson (1957), relative depth is defined as the maximum depth as a percentage of the mean diameter, which is equal to 50 $z_m \sqrt{\pi}(\sqrt{A})^{-1}$.

[3]Following Hutchinson (1957). Bottom temperatures greater than 5 C are considered to represent significant warming.

[4]Dominants are defined as species constituting more than 10% by number of the estimated total May standing crop.

TABLE 1. Some physical and chemical features of the 15 ELA lakes selected for zoobenthic studies. Arrangement of lakes within categories is in order of increasing relative depth. Temperature and oxygen readings are from July or August and, unless indicated otherwise, are from 0.5 to 1.5 m off the bottom. Data incorporated in this table are primarily from Brunskill and Schindler (1971) and Schindler (1971).

Lake category	Lake	Surface area (*ha*)	Maximum depth (z_m, *m*)	Mean depth ($\bar{z}$, *m*)	Relative depth (z_r, %)	Summer bottom temp (*C*)	Summer bottom oxygen (*mg/liter*)	Stratification type
A	303	9.93	2.5	1.5	0.70	14.3	8.2	III
B	81	1.3	−7	−3	5.44	4.3	0.1	I
	241	1.75	12.5	5.5	8.37	4.9	0.0	Meromictic
	230	1.67	13.6	6.2	9.33	4.0	0.1	I
C	132	7.17	8.4	3.3	2.78	10.5	5.3	III
	304	3.62	6.7	3.2	3.12	7.4	0.0	II
	261	5.57	9.6	2.9	3.60	5.7	0.1	II
	227	5.00	10.0	4.4	3.96	4.4	0.1	I
D	240	44.1	13.1	6.1	1.75	7.3	0.6	II
	302	23.7	13.8	5.4	2.51	5.3	0.1	II
	122	12.2	12.8	7.2	3.25	4.0	2.9[a]	I
E	465 (Mad Dog)	−181	−30	−15	1.98	5.1	5.5	II
	239	56.1	30.4	10.5	3.60	4.8	4.1	I
	305	52.0	32.7	15.1	4.02	4.8	7.8	I
F	161 (Hillock)	−1008	−117	−40	3.27	4.1	8.8	I

[a]Sample from 2.8 m off the bottom.

organisms (those constituting more than 10% of the total) were always species of Diptera in the smaller lakes and always *Pontoporeia affinis* (an amphipod) and *Pisidium conventus* (a sphaeriid) in the larger deeper lakes. In categories C, D, and E, an increase in the relative depth invariably coincided with a reduction in the estimated standing crop.

As outlined in Table 3 many of the nonchironomid species found in ELA lakes are, presumably because of their environmental requirements, present in only a small percentage of the lakes. Not surprisingly *P. affinis*, *Mysis relicta*, and *P. conventus* were essentially restricted to large lakes with cold well-oxygenated hypolimnetic waters. In contrast, two of the chaoborines, *Chaoborus brunskilli* and *C. americanus*, were restricted to the small, relatively deep (z_r = 5.44–9.33), and colored lakes that have cold deoxygenated water below the thermocline. Another species of *Chaoborus*, *C. albatus*, was found only in lake 303, a shallow unstratified lake, whereas *Chaoborus flavicans* and *C. punctipennis* were found primarily in the more intermediate lakes (categories B and D). The apparent habitat selection on the part of species of *Chaoborus* was somewhat unexpected. Cook (1956) and Stahl (1966) considered that the species in this genus were quite capable of living in a wide variety of lentic habitats.

Chironomidae were present in lakes of all categories (Table 4) and were particularly abundant in shallow well-oxygenated basins such as those found in lakes 132 and 303. Some taxa, including *Polypedilum* cf. *nubeculosum*, *Psectrocladius* spp., and *Pagastiella* sp., were not present in samples from any of the deeper lakes. *Pagastiella* is extremely abundant in Marion Lake, a shallow lake in British Columbia (Hamilton MS 1965), but has not previously been recorded from elsewhere in North America.[5] The deepwater species *Heterotrissocladius subpilosus* was found only in lake 161 (Hillock), the most oligotrophic of the 15 lakes investigated (Brunskill and Schindler 1971; Schindler and Holmgren 1971). Brundin (1958) considers that this species is the best indicator of ultraoligotrophic conditions in northern European lakes.

A mathematical index, the percentage similarity of community (PS_c), was used to obtain a numerical measure of the similarities between the benthic communities in these lakes. This index is calculated as follows:

$$PS_c = 100\text{–}0.5 \Sigma |a\text{–}b| = \Sigma \min (a,b),$$

[5]*Paralauterborniella ostansus* Webb, recently described from Costello Lake, Ont., by Webb (1969), appears to be a typical *Pagastiella*.

TABLE 2. Selected aspects of the bottom fauna of some ELA lakes. Arrangement of lakes within categories is again in order of increasing relative depth.

Lake category	Lake	Relative depth (z_r, %)	Total no. per m²	% Diptera	% Amphipoda	% Sphaeriidae	Dominant (D) and indicator (I) organisms[a] for lake category
A	303	0.70	2946	97.8	0	1.5	D: *Polypedilum* cf. *nubeculosum* D: *Procladius* spp. I: *Chaoborus albatus*
B	81	5.44	104	85.7	0	0	DI: *Chaoborus brunskilli*
	241	8.37	461	93.5	3.2	0	D: *Procladius* spp. D: *Phaenopsectra coracina*
	230	9.33	236	93.8	0	0	D: *Polypedilum* cf. *nubeculosum* I: *Chaoborus americanus*
C	132	2.78	3556	96.9	0.7	1.1	D: *Chaoborus flavicans*
	304	3.12	1734	93.3	0	5.8	D: *Microtendipes* sp.
	261	3.60	911	99.2	0	0	D: *Chaoborus punctipennis*
	227	3.96	672	96.1	0	2.6	D: *Chironomus* cf. *anthracinus*
D	240	1.75	1642	88.9	6.8	1.4	D: *Chaoborus flavicans* D: *Chaoborus punctipennis*
	302	2.51	768	93.6	0	0	D: *Phaenopsectra coracina*
	122	3.25	518	89.7	0	5.1	
E	465 (Mad Dog)	1.98	2921	30.1	31.4	21.7	DI: *Pontoporeia affinis*
	239	3.60	2654	19.1	45.3	24.6	DI: *Pisidium conventus*
	305	4.02	2454	11.2	68.5	15.7	I: *Mysis relicta*
F	161 (Hillock)	3.27	1699	15.2	54.4	27.1	DI: *Pontoporeia affinis* DI: *Pisidium conventus* I: *Heterotrissocladius subpilosis* I: *Mysis relicta*

[a]Dominants are arranged within categories in decreasing order of abundance and are considered as any taxa making up more than 10% by number of the estimated total May standing crop. Indicator organisms are taxa that consistently occur in lakes falling in one or more categories and for some reason or other appear to be absent from other categories. Indicator organisms may or may not be dominants.

where a and b are, for each taxon, the percentage of the total animals in samples from lakes A and B respectively. The taxonomic divisions used for calculating this index are those in Tables 3 and 4. High PS_c values are generally indicative of a high similarity between the samples being compared. As outlined in Table 5, PS_c values within categories ranged from 23 to 72 with a mean of 51 (n = 15). The comparable values for the between-category comparisons were 0–70 with a mean value of 18 (n = 90). Most between-category comparisons were consistently low, indicating that the zoobenthos in the lakes of different categories were generally quite distinctive. Comparisons between adjacent categories did, however, tend to result in relatively high PS_c values. This was particularly true with comparisons between categories C and D and between categories E and F. These very high values (means of 41 and 66 respectively) are a reflection of the many taxa shared by these groups of lakes.

In general the results reported here are consistent with those reported elsewhere in the literature. The benthic fauna in ELA lakes, even at the species level, bears a resemblance to the fauna found in many Swedish shield lakes (Brundin 1949). The general shift, with increasing depth, from a pre-

TABLE 3. Estimated early May densities (numbers/m²) of benthic macroinvertebrates (excluding Chironomidae) in some ELA lakes. Arrangement of lakes within categories is in order of increasing relative depth. Organisms arranged approximately in order of their abilities to live in deep water.

Lake category:	A	B			C				D			E			F
Lake:	303	81	241	230	132	304	261	227	240	302	122	465	239	305	161
No. samples:	7	3	3	6	10	5	6	10	10	10	10	10	10	10	11
Chaoborus albatus Johnson	25	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pisidium casertanum (Poli)	13	–	–	–	27	27	–	–	–	–	–	9	–	–	–
Gammarus lacustris Sars	–	–	15	–	27	–	–	–	–	–	–	–	–	–	–
Chaoborus brunskilli Saeth.	–	74	74	111	–	–	–	–	–	–	–	–	–	–	–
Chaoborus americanus (Joh.)	–	15	–	30	–	–	–	–	–	–	–	–	–	–	–
Chaoborus flavicans (Meig.)	–	–	–	44	2224	–	104	186	315	297	58	–	–	–	–
Chaoborus punctipennis (Say)	–	–	–	22	–	551	326	213	373	186	44	466	4	71	–
Juvenile *Pisidium*	32	–	–	–	13	53	–	13	22	–	9	93	617	315	32
Oligochaeta	6	–	–	–	13	18	7	–	49	40	22	431	151	93	44
Pontoporeia affinis Lind.	–	–	–	–	–	–	–	–	111	–	–	919	1203	1685	925
Mysis relicta Loven	–	–	–	–	–	–	–	–	–	–	–	13	18	9	4
Pisidium conventus Clessin	–	–	–	–	–	–	–	–	–	–	–	533	31	71	428
Others (excluding Chironomidae)	19	15	30	15	49	62	–	9	4	9	31	44	138	9	12
Total (excluding Chironomidae)	95	104	119	222	2353	711	437	421	874	532	164	2508	2162	2253	1445

dominantly dipteran fauna to one consisting largely of the amphipod *P. affinis* coincides with findings reported from other lakes on the Canadian Shield (Oliver 1960; Slack 1967). The relations that, in ELA lakes, apparently exist between the benthic faunas and the physical and chemical conditions of the lakes they inhabit will probably have some application to other small Canadian Shield lakes.

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TABLE 4. Estimated early May densities (numbers/m²) of Chironomidae in some ELA lakes. Arrangement of lakes within categories is in order of increasing relative depth. Organisms arranged approximately in order of their abilities to live in deep water.

Lake category:	A	B			C				D			E			F
Lake:	303	81	241	230	132	304	261	227	240	302	122	465	239	305	161
No. samples:	7	3	3	6	10	5	6	10	10	10	10	10	10	10	11
Polypedilum cf. *nubeculosum* (Meigen)	2502	–	89	0	9	9	–	44	–	–	–	–	–	–	–
Psectrocladius sp.	6	–	–	–	–	27	37	–	–	–	–	–	–	–	–
Pagastiella sp.	–	–	–	–	–	9	22	–	–	–	–	–	–	–	–
Microtendipes sp.	–	–	–	–	728	240	126	–	–	–	–	–	31	–	–
Chironomus spp.[a]	–	–	30	7	102	267	252	155	27	89	–	–	–	–	–
Procladius spp.	318	–	104	7	191	124	37	31	147	58	93	–	–	4	–
Heterotrissocladius sp. A	–	–	–	–	–	–	–	–	4	–	18	–	22	–	–
Chironomus cf. *atritibia* Malloch	–	–	–	–	84	–	–	–	62	80	75	138	164	84	69
Phaenopsectra coracina (Zett.)[b]	–	–	89	–	18	–	–	13	422	–	142	93	98	18	89
Tanytarsini spp.	–	–	–	–	27	196	–	4	102	9	13	169	155	89	48
Protanypus sp.[b]	–	–	15	–	–	–	–	–	–	–	–	13	22	4	4
Heterotrissocladius subpilosus (Kieff.)[b]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	44
Other Chironomidae	25	–	15	–	44	151	–	4	4	–	13	–	–	4	–
Total Chironomidae	2851	–	342	14	1203	1023	474	251	768	236	354	413	492	203	254

[a]At least two species, including *C. anthracinus* Zett. and *C. attenuatus* Walk., are included in this category.
[b]These species were already emerging at the time of sampling and consequently the density estimates are probably low.

TABLE 5. Percentage similarity of community (PS_c) for the zoobenthic populations of 15 lakes in ELA. The figures above the diagonal line are comparisons between individual lakes, those below the line are averages of values between and within lake categories.

		Category														
		A	B			C				D			E			F
Category	Lake	303	81	241	230	132	304	261	227	240	302	122	465	239	305	161
A	303		1	32	4	8	11	5	13	11	9	14	2	2	2	2
B	81			23	66	1	–	–	1	–	1	6	2	5	–	1
	241	12	39		29	13	21	11	21	30	15	46	5	10	2	6
	230					26	19	33	35	39	35	29	11	5	4	1
C	132						27	33	39	31	52	24	6	7	5	5
	304	9		15				68	57	40	46	27	27	15	11	6
	261						49		70	43	52	28	17	2	4	1
	227									52	70	30	22	6	7	5
D	240										59	66	40	25	22	23
	302	11		22			41			56		44	28	14	12	9
	122												26	25	16	17
E	465													58	53	65
	239	2		5			11				23		61		72	63
	305															70
F	161	2		3			4				16			66		

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Preliminary Characterization of Lakes in the Experimental Lakes Area, Northwestern Ontario, Using Diatom Occurrences in Sediments[1]

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STOCKNER, J. G. 1971. Preliminary characterization of lakes in the Experimental Lakes Area, northwestern Ontario, using diatom occurrences in sediments. J. Fish. Res. Bd. Canada 28: 265–275.

Diatoms in deepwater surface sediment from 16 Experimental Lakes Area (ELA) lakes of varying size and morphometry were separated for analysis on the basis of their generally understood habitat preference into littoral and planktonic groups. The lakes were ranked in order of increasing relative abundance of littoral diatoms recovered from deepwater surface sediment. A significant correlation was found between the abundance of littoral diatoms in deepwater sediments and the morphometric variables: lake surface area (A_o), and shoreline length to lake volume (L/V), and percent littoral development in each lake. The Centrales was the dominant planktonic group in most of the ELA lakes examined. Species of *Cyclotella* and *Melosira* were the dominant diatoms in most ELA lakes. The ratio of the two planktonic groups — Araphidineae and Centrales (A/C) — calculated from sediment counts, agreed closely with the A/C ratio enumerated from 1969 phytoplankton counts in two lakes compared. Based on a lake classification scheme using values of the A/C ratio from sediment diatom counts, the majority of ELA lakes were classed as oligotrophic. Analysis of a 155-cm core from lake 240 showed little change in diatom species composition over the past 3000–4000 years. Centrales was the dominant diatom assemblage at all sediment depths. The dominant diatoms in the sediment of lake 240 and the majority of ELA lakes examined were similar to those dominant in the deepwater sediments of well-studied oligotrophic lakes in other lake districts. On the basis of calculated A/C ratios in surface sediment in several lakes at temperate latitudes, a lake trophic classification is proposed.

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MUCH can be learned about the developmental history of a lake by studying the distribution and succession of limnologically important microfossils in lake sediment. Pertinent watershed changes, resulting from forest fire, land clearance, and climatic amelioration, that lead directly to vegetational changes can often be effectively ascertained by sediment pollen analyses. Human-induced watershed disturbance that causes changes in the erosion of biologically important nutrients from the catchment basin or leads to a direct discharge of effluents into a lake can markedly affect both littoral and planktonic communities. These changes occurring within a lake can best be assessed by diatom or cladoceran microfossil analyses. The best available reconstruction of the developmental history of a lake and its watershed is achieved by a combination of both approaches (Pennington 1943, 1947; Kendall 1969). The distribution of microfossils in near-surface sediment has been used to interpret recent changes in species composition and community succession in lakes as they relate to changes in trophic state caused by man-induced environmental change (Nipkow 1927; Wuthrich 1961; Stockner and Benson 1967; Davis 1967).

The purpose of this study was to identify the dominant diatom assemblages in surface sediment from 16 undisturbed Precambrian Shield lakes of varying morphometry and in a short core from Experimental Lake Area (ELA) lake 240. Attempts were made to relate the sedimentary abundance of both planktonic and littoral diatom groups in these lakes to observations from other temperate lakes, so as to assess their position on a trophic scale. To date, the ELA lakes have been little affected by man's activities, and therefore results of this study, as well as future paleolimnological

[1]The twelfth in a series of 14 papers on the work of the Fisheries Research Board of Canada, describing background environmental data on the Experimental Lakes Area, northwestern Ontario. For location of numbered lakes see insert map at the back of this issue of the Journal of the Fisheries Research Board of Canada. A key to lake locations is given by Cleugh and Hauser (1971).

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and phycological work, should provide meaningful baseline data in relation to future natural or artificial changes.

Methods

Surface sediment was taken from Ekman dredge samples obtained in areas of maximum depth from 16 lakes[2] (lakes are listed in Fig. 1). A 155-cm sediment core was taken with a gravity corer from lake 240 (insert map coordinates E.2–6.3) at a water depth of 9 m. An hour after being taken, the core was extruded and sectioned at 10-cm intervals. Samples were obtained from the nonsmeared inner portion of each 10-cm section and the remaining material was refrigerated in plastic bags. Water content was determined by drying refrigerated samples at 105 C for 16 hr. Loss of weight on ignition values were obtained by burning oven-dried samples in a muffle furnace at 500 C for 4 hr.

Approximately 1 g of fresh sediment from each of the 16 Ekman samples and the core samples was macerated in concentrated nitric acid diluted 1:1 with distilled water. Samples were boiled until they reached half the original volume, then $K_2Cr_2O_7$ was added for final oxidation. The samples were repeatedly decanted, rinsed, and allowed to resettle until no trace of acid remained. Permanent slides were made using Permount mounting medium. Duplicate counts of approximately 200–250 diatom frustules per slide were made under 1000× magnification. The monographs of Hustedt (1930), Cleve-Euler (1951), and Patrick and Reimer (1966) were used for species identification. The more common diatoms were identified to species, others to genera.

Data were processed on an IBM 360 at the University of Manitoba Computer Center. Output gave percentage composition of the total diatom population for all species, the order Centrales, and the four pennate tribes represented. Computer output data for the relative abundance of each species, genus, and group enumerated from the sediment core were plotted by a Calcomp digital plotter as a function of sediment depth.

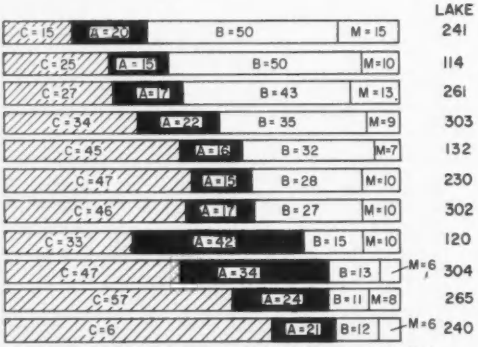

FIG. 1. Percent relative abundance of diatoms in surface sediment from 16 ELA lakes. A, Araphidineae; B, Biraphidineae; C, Centrales; M, Monoraphidineae–Raphidioidineae.

[2]For location see Cleugh and Hauser (1971), and for morphometric data Brunskill and Schindler (1971).

Results and Discussion

Diatoms in Deepwater Surface Sediment, 16 ELA Lakes

Two basic types of diatom occur in the aquatic environment: round (order Centrales) and elongate, symmetrical to the longitudinal axis (order Pennales). On the basis of the number of raphe and their location and morphology on the frustule, the order Pennales can be further subdivided into four tribes (after Fott 1959; Engler 1954): Araphidineae (A), Biraphidineae (B), Monoraphidineae (M), and Raphidioidineae (R). The tribe Araphidineae (A) and the order Centrales (C) consist chiefly of planktonic species; the majority of littoral diatoms in lakes belong to the pennate tribes B, M, and R. One important prerequisite to growth and reproduction for the majority of the littoral diatoms is a suitable substrate such as rock, mud, sand, or aquatic macrophyte. Other more obvious factors include light and an adequate supply of nutrients. The diatoms in the deepwater surface sediment of the 16 ELA lakes examined were separated into groups for analysis, and on the basis of their relative abundance the basic similarities and differences in diatom composition among lakes are discussed.

Littoral diatoms

Counts of littoral diatoms from deepwater surface sediment of the 16 ELA lakes were arranged in order of increasing abundance of groups B and M (for presentation group R was included in group M — Fig. 1). Familiar genera commonly encountered in all ELA lakes include: B: *Navicula*, *Anomoeoneis*, *Gomphonema*, *Nitzschia*, *Cymbella*; M: *Achnanthes*, *Cocconeis*; R: *Eunotia*.

The littoral species *Anomoeoneis serians* and *Achnanthes minutissima* were found consistently in the sediment of all lakes examined. Little is known of the ecology of *A. serians* or *A. minutissima*, but their common occurrence in the littoral regions of the ELA lakes (see Stockner and Armstrong 1971) and in other oligotrophic lakes (Lund 1968;

Fox et al. 1969) indicates that they can sustain good growth and reproduction in nutrient-poor waters. Species of the genus *Eunotia* were common in the sediment of only lake 241. *Eunotia* is generally considered an acidophilic genus (Jorgenson 1948; Foged 1954) and is often common in bogs. The surface water *p*H of lake 241 is between 5 and 6, among the lowest of the lakes currently under investigation. With the exception of lake 241, the other lakes examined were very similar with respect to the composition of sedimented littoral diatoms.

Some ELA lakes had considerably more littoral diatoms in deepwater sediment (Fig. 1). The abundance of littoral, in relation to planktonic diatoms in deepwater sediment is primarily a reflection of the extent of littoral development, which is in turn dependent upon lake morphometry and water transparency.

This relation can be seen by plotting the relative abundance of littoral diatoms (groups B, M, and R) as a function of the littoral development in each lake (Fig. 2). Morphometric data are incomplete for some lakes but for 10 lakes tested the relation is highly significant ($r^2 = 0.92$, $P = 0.01$). Two lakes, 241 and 230, are also represented in the figure but both are in sheltered, small, and overdeepened basins. If lake 230 is included in the analysis the relation is still significant ($r^2 = 0.79$, $P = 0.05$), but if lake 241 is included the relation is no longer significant ($r^2 = 0.12$, NS). Since the surface sediment of each lake came from areas of maximum depth, valid cross-comparisons among lakes with respect to diatom composition and morphometric data can be made.

By multiple linear regression analyses, a number of other lake morphometric and physico-chemical factors were tested to objectively assess their relation to the observed littoral diatom distribution in the deepwater sediments of ELA lakes. Independent variables tested were (from Brunskill and Schindler (1971) and Schindler (1971)): (*a*) lake surface area (A_o), (*b*) mean depth (*z*), (*c*) length of shoreline (L), (*d*) length of shoreline/lake volume (L/V), (*e*) Secchi disc (mean summer value), and (*f*) color (Hazen units). The only variables significantly correlated with the abundance of littoral diatoms in deepwater sediment were: lake surface area (A_o) and length of shoreline/lake volume (L/V) (Table 1). The amount any given lake is sheltered from prevailing winds would also seem to be an important consideration, but such data were not available and could therefore not be included in the analysis.

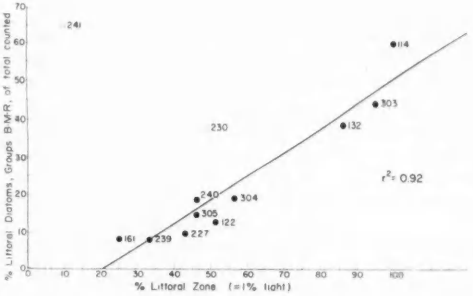

FIG. 2. Relation between percent littoral diatoms recovered from deepwater surface sediment and percent littoral development in each lake. Lakes 241 and 230 are plotted but not included in regression analysis.

From the analyses of littoral diatoms in the deepwater sediments of 16 ELA lakes of varying morphometry, these salient points emerge: (*a*) in small (<5 ha) lakes with well-developed littoral regions, littoral standing crop may surpass limnetic standing crop, and the greater contribution of littoral diatoms, as opposed to planktonic in deepwater sediment, is accordingly an indication of the importance of the littoral community in these lakes, e.g., lakes 114, 303, and 132; (*b*) in lakes with area >5 ha, littoral standing crop relative to limnetic diminishes in importance, until gradually, in large deep lakes, littoral algal standing crop is but a minor portion of the total algal production of the lake, and the abundance of the diatom groups B, M, and R, in relation to the planktonic groups A and C, in the deepwater sediments is accordingly small, e.g., lakes 239, 240, 305, and 161.

The deposition of littoral diatoms in deepwater sediments of a lake is directly related to wind-driven turbulence and to the slope of the shoreline. The extent of deposition, resuspension, and redeposition of littoral diatoms is not known, but the mechanism is undoubtedly similar to that postulated by Davis (1968) for pollen. Due to the high specific gravity of diatom frustules, especially

TABLE 1. Results of the multiple linear regression analysis regarding the abundance of littoral diatoms (A_{Ld}) groups B, M, R, to lake morphometric factors (A_{Ld} = % of total enumerated in 1 cc sediment).

$A_{Ld} = 0.096\ S/V - 17.65\ A_o + 23.93$		
t value of partial regression coefficient	2.603	−1.586
Standard partial regression coefficient	1.454	−0.886
Coefficient of multiple determination	$R^2 = 0.54$; $F = 5.32$ S*; df 2 & 9	

*S = significant, 0.05 level.

littoral ones, much less disturbance and redeposition would occur than for the lighter pollen grains or planktonic diatom frustules. It follows that if the littoral zone is enlarged, either by increased transparency or by significant fluctuations in water level, then as the lake ages and becomes shallower, a proportionately greater input of littoral diatoms to deepwater sediment is to be expected. This developmental stage, frequently representing the final one in the existence of a lake, has been well documented by the paleolimnological studies of Patrick (1943, 1954) in Linsley Pond and Bethany Bog, Conger (1939) in Crystal Lake, and Yuse (1966) and Korde (1966a) in several Russian lakes.

The previous comparison of littoral algal abundance among lakes included only the groups B, M, and R, which by substrate dependence are almost exclusively limited to littoral regions. Other diatoms, chiefly *Cyclotella stelligera* and *Tabellaria flocculosa*, may commence growth in the spring in the littoral regions, forming chains, but are eventually dispersed by wave action or general turbulence and become part of the plankton. In this discussion these species are considered as planktonic. A good example of this is provided by counts of *C. stelligera* in both littoral and planktonic habitats in lake 240 in 1969. Peak abundance was observed in the littoral in late May, but by the middle of June they were rarely encountered. In the plankton, the pulse of *C. stelligera* commenced in early June and continued into the first week of July (S. K. Holmgren personal communication). Thus, the decline of populations in the littoral coincided with rapid increases in the plankton. *Tabellaria flocculosa* showed a similar pattern, but with a 1-week lag period.

Planktonic diatoms

In most all of the 16 ELA lakes examined there was a preponderance of planktonic diatoms, groups A and C, over littoral ones (Fig. 1). The five dominant diatom species encountered in the surface sediment of each lake are presented in Table 2. The dominant planktonic diatoms in the surface sediment of most lakes were, in decreasing order of abundance: *C. stelligera* (C), *Melosira italica* (C), *Cyclotella kützingiana* (C), *Rhizosolenia longiseta* (C), *Tabellaria fenestrata* (A).

These species commonly occur in oligotrophic lakes and are seldom abundant in eutrophic lakes (Jarnefelt 1952; Pearsall 1932). The dominant diatom genus in most ELA lakes was *Cyclotella*. Rawson (1956) reported *Cyclotella* as an indicator of oligotrophic waters in northern Canadian lakes and Foged (1954) and Jarnefelt (1952) found it to be abundant in oligotrophic lakes in Denmark and Finland. Stockner (unpublished data) found it to be the dominant diatom genus in the sediments of Wastwater and Ennerdale, the most oligotrophic lakes in the English Lake District. Yuse (1966) considers *Cyclotella* as the pioneer genus of the Late and Postglacial lake phytoplankton populations, and by direct inference a diatom requiring little nutrients. Its dominance in the sediments during the oligotrophic stage of Lake Somino, USSR (Kosirenko 1961, as cited in Yuse 1966), and in the present plankton of Lake Baikal (Popowskaya 1960, 1961) is further evidence of its ability to sustain good growth and reproduction in nutrient-poor waters. Clearly, *Cyclotella* is a reliable character form of oligotrophic waters. There are a few exceptions, the most notable being *Cyclotella meneghiniana*, which often occurs in mesoeutrophic water (Stockner and Benson 1967). *Cyclotella meneghiniana* rarely occurs in oligotrophic lakes and was not observed in any of the 16 ELA lakes examined.

The ratio of Araphidineae to Centrales (A/C) calculated from deepwater sediment counts appears to accurately depict the importance of each diatom group in the plankton of the lake. There was good agreement between the A/C ratio of plankton counts and the A/C ratio obtained from the sediments of lakes 240 and 305 (Table 3). The A/C ratios of the plankton, obtained by summing all counts at each depth on each date from January to November 1969, were 0.28 and 0.53, respectively. Sediment values, representing a long-term running average, were 0.34 in lake 240 and 0.35 in lake 305. Thus, A/C counts from sediments provide a quick, yet reasonably accurate estimate of the relative importance of each group in the plankton.

Lake 240 Core Analysis

Physical-chemical features

The top 5 cm of the core were unconsolidated; remaining portions held their shape upon extrusion. There were no visible laminations in the 155-cm core. In an 8-m core[3] obtained concurrently, laminated clays appeared from 5.5 to 6.0 m, and the remaining portion consisted of unlaminated silt and clay. The postglacial sediment was a green-brown color and had a smooth, pastelike consistency. The water content of the 155-cm core was approximately 85–90%, and roughly 20% of the solid phase was lost on ignition (Fig. 3). Chemical

[3]Core obtained with a Livingstone corer by Dr J. H. McAndrews, Royal Ontario Museum, Toronto, Ont. Palynological studies of this core and another core from lake 114 are currently in progress.

TABLE 2. Five most commonly encountered diatoms in the surface of deepwater sediment of 16 ELA lakes.

Lake 120	Lake 302
Asterionella formosa Hass.	*Cyclotella stelligera* Cl. et Grun.
Tabellaria fenestrata (Lyngb.) Kütz.	*Fragilaria pinnata* Ehr.
Melosira italica (Ehr.) Kütz.	*Navicula sphaerocephala* A. Berg
Fragilaria construens (Ehr.) Grun.	*Cyclotella kützingiana* Thwaites
Cyclotella stelligera Cl. et Grun.	*Synedra acus* Kütz.
Lake 230	Lake 261
Cyclotella stelligera Cl. et Grun.	*Melosira italica* (Ehr.) Kütz.
Tabellaria fenestrata (Lyngb.) Kütz.	*Fragilaria construens* (Ehr.) Grun.
Anomoeoneis serians (Bréb.) Cleve	*Neidium affine* (Ehr.) Cleve
Pinnularia biceps Greg.	*Pinnularia biceps* Greg.
Fragilaria construens (Ehr.) Grun.	*Anomoeoneis serians* (Bréb.) Cleve
Lake 303	Lake 240
Cyclotella stelligera Cl. et Grun.	*Melosira italica* (Ehr.) Kütz.
Synedra acus Kütz.	*Cyclotella stelligera* Cl. et Grun.
Fragilaria construens (Ehr.) Grun.	*Tabellaria fenestrata* (Lyngb.) Kütz.
Anomoeoneis serians (Bréb.) Cleve	*Asterionella formosa* Hass.
Nitzschia fonticola Grun.	*Synedra acus* Kütz.
Lake 239	Lake 227
Cyclotella stelligera Cl. et Grun.	*Rhizosolenia longiseta* Zach.
Rhizosolenia longiseta Zach.	*Cyclotella stelligera* Cl. et Grun.
Synedra acus Kütz.	*Synedra acus* Kütz.
Asterionella formosa Hass.	*Tabellaria flocculosa* (Roth) Kütz.
Tabellaria fenestrata (Lyngb.) Kütz.	*Fragilaria construens* (Ehr.) Grun.
Lake 305	Lake 241
Cyclotella stelligera Cl. et Grun.	*Melosira islandica* (Bréb.) Cleve
Cyclotella kützingiana Thwaites	*Anomoeoneis serians* (Bréb.) Cleve
Cyclotella comta (Ehr) Kütz.	*Melosira italica* (Ehr.) Kütz.
Cyclotella ocellata Pant.	*Pinnularia biceps* Greg.
Fragilaria construens (Ehr.) Grun.	*Frustulia rhomboides* (Ehr.) de Toni
Lake 132	Lake 265
Cyclotella stelligera Cl. et Grun.	*Cyclotella stelligera* Cl. et Grun.
Nitzschia sublinearis Hust.	*Cyclotella kützingiana* Thwaites
Pinnularia biceps Greg.	*Synedra acus* Kütz.
Stauroneis anceps Ehr.	*Rhizosolenia longiseta* Zach.
Tabellaria fenestrata (Lyngb.) Kütz.	*Achnanthes minutissima* Kütz.
Lake 304	Lake 114
Cyclotella stelligera Cl. et Grun.	*Anomoeoneis serians* (Bréb.) Cleve
Synedra acus Kütz.	*Pinnularia* spp.
Rhizosolenia longiseta Zach.	*Achnanthes minutissima* Kütz.
Pinnularia biceps Greg.	*Synedra acus* Kütz.
Neidium affine (Ehr.) Cleve	*Cyclotella stelligera* Cl. et Grun.
Lake 161	Lake 122
Cyclotella kützingiana Thwaites	*Melosira italica* (Ehr.) Kütz.
Cyclotella ocellata Pant.	*Rhizosolenia longiseta* Zach.
Cyclotella comta (Ehr.) Kütz.	*Cyclotella stelligera* Cl. et Grun.
Cyclotella stelligera Cl. et Grun.	*Coscinodiscus subvelatus* A. Schmidt
Melosira italica (Ehr.) Kütz.	*Tabellaria flocculosa* (Roth) Kütz.

TABLE 3. A/C ratio in sediment and plankton counts, lakes 240 and 305.

	% total[a] diatoms	A/C
Lake 240		
Plankton		
Centrales (C)	0.78	0.28
Araphidineae (A)	0.22	
Sediment		
Centrales (C)	0.61	0.34
Araphidineae (A)	0.21	
Lake 305		
Plankton		
Centrales (C)	0.65	0.53
Araphidineae (A)	0.35	
Sediment		
Centrales (C)	0.61	0.35
Araphidineae (A)	0.22	

[a]Includes total of group A and C count. No diatoms belonging to groups B, M, or R were found in the plankton.

analyses of the surface sediment of some of the lakes discussed in the previous section are presented by Brunskill et al. (1971).

The length of sediment above the clay-till boundary in lake 240 was 5.5 m, representing a sediment accumulation over a period of 10,000–12,000 years (Brunskill and Schindler 1971; Zoltai 1961). By interpolation the average yearly sedimentation rate for lake 240 is between 0.4 and 0.6 mm/year. This estimate assumes an even deposition over a given time span that is unlikely to occur in any lake. Furthermore, compaction and variation in water content are not taken into account. Allowing for error due to these factors, the results of the analysis of this 155-cm core can be broadly viewed to represent events occurring during the past 2500–3750 years.

Diatom assemblages, lake 240 core

Species composition — Dominant diatoms in the sediments of lake 240 were *C. stelligera*, *M. italica*, *A. minutissima*, and *Fragilaria construens*. In total about 30 species were identified. These diatoms were essentially the same as those now commonly occurring in the plankton (S. K. Holmgren, personal communication) and in the littoral regions of the lake (Stockner and Armstrong 1971). The only obvious shift in the relative abundance of sedimented diatom species occurred above 50 cm, 800–1250

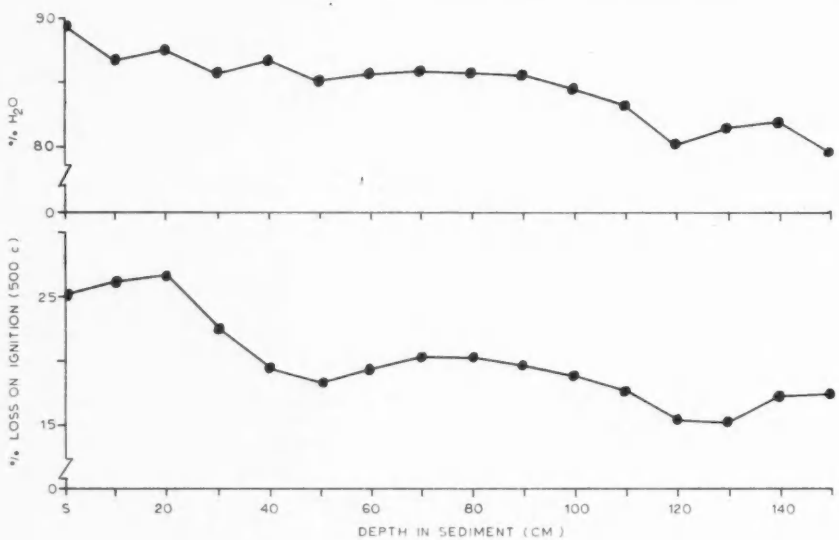

FIG. 3. Water content and loss on ignition from a 155-cm sediment core, lake 240.

years before present (B.P.). Below 50 cm *F. construens*, *F. pinnata*, and *M. italica* were common; *Cyclotella* spp. increased markedly in the more recent surface sediment. With this exception the species distribution at the surface was similar to that observed at 155 cm. Reasons for the observed changes at 50 cm cannot at present be given. It is likely that palynological studies currently under way will elucidate possible edaphic or climatic factors that were responsible for the observed species shifts at this sediment depth. Forest fires that swept the area 50 and 100 years ago (S. C. Zoltai, personal communication) left no obvious markers in near-surface sediment (5–10-cm level), and though fine sectioning (1-cm intervals) of the core was not undertaken, the similarity of diatom species distribution from 10 cm to the surface tentatively indicates that the forest fires did not have an appreciable long-term effect on the diatom flora of lake 240.

Species groups — It is instructive to compare the sediment depth distribution of the planktonic diatom groups A and C in lake 240 sediments with similar data from sediment core analyses of other lakes at temperate latitudes, some of which have undergone marked changes caused by man's activities within their watersheds.

Centric diatoms (C) are the major group enumerated from the 155-cm core from lake 240. There is little change with increasing sediment depth in the relative abundance of the diatom groups in the core (Fig. 4A). This is not surprising since the watershed has not been affected by man's activities. Reindeer Lake, a large Shield lake in northern Manitoba–Saskatchewan (see Rawson 1960 for a description) has not been appreciably affected by human activities on its watershed, and shows, as lake 240, a dominance of Centrales (Fig. 4B). Wastwater, in the English Lake District, shows a distribution of groups A and C that is similar to both lake 240 and Reindeer Lake (Fig. 4C). There are several orders of magnitude difference in size between these three lakes, lake 240 being the smallest and Reindeer the largest. However, they share two common characteristics, which as here hypothesized produce the observed plankton diatom community similarities: (*a*) watersheds relatively free of significant human disturbance; and (*b*) nutrient-poor waters.

The effects of man-induced watershed disturbance on the A/C ratio is seen by comparing the oligotrophic lake 240, Reindeer, and Wastwater with the meso-eutrophic Lake Washington and Windermere South Basin. In Lake Washington the A group increased markedly after human watershed disturbance and sewage discharge whereas C diminished to the point of rarity (Fig. 4D). The watershed of Windermere South Basin has been subject to human disturbances, chiefly from deforestation, agricultural fertilization, and sewage discharge. These factors have caused, as in Lake Washington, a striking increase in the relative abundance of A (Fig. 4E).

A tabulation of the most common diatoms found in cores from each of the lakes compared here further accentuates the basic similarity of planktonic diatoms among lakes both past and present (Table 4). *Cyclotella* spp. and *M. italica* are at present common in lake 240, Reindeer, and Wastwater, and were the common diatoms in the oligotrophic stage of Lake Washington and Windermere South Basin prior to watershed disturbance, i.e., at a sediment depth below 15 and 20 cm, respectively.

The cultural eutrophication of Lake Washington led to a marked increase in populations of *Fragilaria crotonensis*, and in the South Basin of Windermere populations of *Asterionella formosa* showed initial increases after watershed disturbance in the late 19th century, later followed by increases of *F. crotonensis*. The increases in *F. crotonensis* coincide with the gradual buildup of sewage discharge into the South Basin that commenced in 1918 (Stockner unpublished data).

The similarity in the distribution of the diatom groups A and C between lake 240, Reindeer, and Wastwater is indicative of a state of trophic equilibrium (Hutchinson and Wollack 1940) preserved and sustained by watershed stability. More simply stated, the watersheds of these lakes have been little affected by man's activities. By comparison, Windermere and Lake Washington have shown striking changes in planktonic diatom species composition due to human watershed disturbance and concomitant cultural eutrophication. From these cross-comparisons it seems reasonable to infer that lake 240 has changed little over the past few thousand years, and can be classed, along with most of the culturally undisturbed Canadian Shield lakes, as oligotrophic.

A Lake Classification Scheme Based on the the Sediment A/C Ratio

The ratio of planktonic groups A/C in sediment counts from deepwater cores appears to be a sensitive indicator of lake trophy (Stockner and Benson 1967). It is based principally on the observation that in most temperate lakes exhibiting accelerated eutrophication caused by man's activities on their watersheds, a major shift in planktonic diatoms occurs, from an initial Centrales dominance toward an increasing abundance of araphidinate diatoms, e.g., Zürichsee (Thomas 1964), Lac Neuchatel (Wuthrich 1961), Windermere

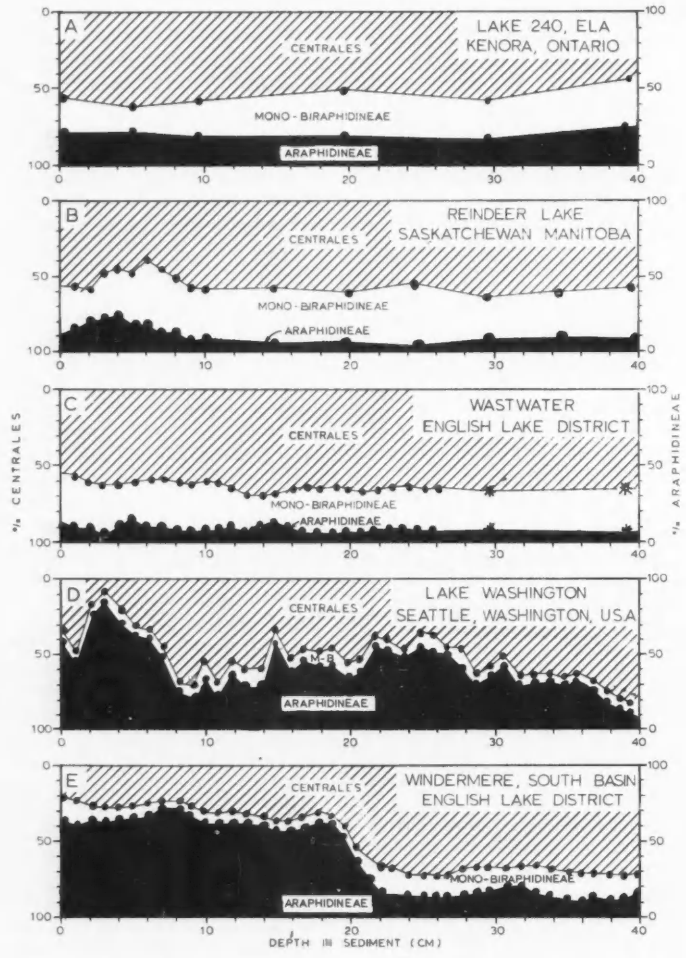

FIG. 4. Percent diatom abundance of groups Centrales, Araphidineae, Biraphidineae and Mono-Raphidioidineae (Mono-Biraphidineae on figure) in near surface sediment. Lakes as listed in figure.

(Pennington 1943; Stockner unpublished data), Lake Washington (Stockner and Benson 1967), and Linsley Pond (Patrick 1943; Stockner unpublished data). The number and variety of species involved in the succession varies, depending upon the lake's geographical location, but for each group often includes the well-known species *M. italica*, *C. stelligera*, *C. ocellata*, *C. comta*, *Stephanodiscus astraea* (Centrales); and *A. formosa*, *Synedra acus*, *S. delicatissima*, *F. crotonensis*, *F. construens*, *T. fenestrata* (Araphidineae).

The A/C ratio of the 16 ELA lakes ranges from 0.07 to 1.33 (Table 5). The average A/C ratio for all ELA lakes examined was 0.53. It is informative to compare A/C ratios obtained from ELA lake sediments with those calculated from sediment counts in other temperate lakes in different lake districts (Table 5).

The average A/C ratio in the deepwater surface sediment (0–20 cm) of Reindeer is 0.29, which is somewhat lower than the average A/C ratio of ELA lakes. The average A/C ratio in deepwater

TABLE 4. Common diatoms in near-surface sediment of lakes compared and discussed in text.

Lake 240, ELA	Reindeer Lake, Man.–Sask.	Wastwater, English Lake District
0–50 cm	0–50 cm	0–25 cm
Melosira italica (Ehr.) Kütz.	*Cyclotella kützingiana* Thwaites	*Cyclotella striata* (Kütz.) Grun.
Cyclotella stelligera Cl. et Grun.	*Cyclotella stelligera* Cl. et Grun.	*Cyclotella glomerata* Bachm.
Tabellaria fenestrata (Lyngb.) Kütz.	*Cyclotella ocellata* Pant.	*Cyclotella comta* (Ehr.) Kütz.

Lake Washington, Seattle, Wash.	Windermere, South Basin, English Lake District
0–30 cm	0–20 cm
Fragilaria crotonensis Kitton	*Asterionella formosa* Hass.
Fragilaria construens (Ehr.) Grun.	*Melosira italica* (Ehr.) Kütz.
Melosira italica (Ehr.) Kütz.	*Fragilaria crotonensis* Kitton
30–100 cm	20–100 cm
Melosira italica (Ehr.) Kütz.	*Cyclotella comta* (Ehr.) Kütz.
Stephanodiscus astraea v. *minutula* (Kütz.) Grun.	*Cyclotella comensis* Grun.
Cyclotella stelligera Cl. et Grun.	*Melosira italica* (Ehr.) Kütz.

sediment of Wastwater and Ennerdale in the English Lake District is also lower than ELA lakes — 0.09 and 0.22, respectively. In the more productive South Basin of Windermere, the average A/C ratio in the top 20 cm of deepwater sediment is 1.73, whereas in the less productive North Basin (Lund 1949) the average in the top 20 cm is 1.01. In the surface (0–20 cm) deepwater sediment of Esthwaite Water, one of the most productive lakes in the English Lake District (J. F. Talling, personal communication), the average A/C ratio is 2.28 (Stockner unpublished data). In Lake Washington, a culturally eutrophic lake, the average A/C ratio in the top 10 cm of sediment is 2.02; in the strata from 10 to 30 cm, 0.77; and from 30 to 50 cm, 0.29.

Based on the observed variations of the diatom ratio A/C in sediments of temperate lakes here compared (Table 5), and from others currently under investigation by the author, the following broad lake trophic distinctions for temperate lakes seem reasonable:

Type	A/C
Oligotrophic	0–1.0
Mesotrophic	1.0–2.0
Eutrophic	>2.0

There are undoubtedly exceptions where this classification scheme does not apply, notably in shallow lakes or bogs and in rivers and their impoundments. In such instances isothermal conditions tend to prevail and benthic diatom populations most often predominate, making the calculation of the planktonic A/C ratio meaningless. Another instance where the classification may not apply is in those lakes that have been mesoeutrophic throughout most of their postglacial history, e.g., prairie lakes. In these lakes, mesoeutrophic planktonic centrics may still maintain a dominant position and be replaced only at certain periods by the rapid response of the araphidinate diatoms after recent man-induced disturbance (J. P. Bradbury, personal communication).

The literature is replete with examples of various typological schemes used to classify the trophic character of lakes on the basis of either single or multiple characteristics. Many of these are summarily discussed by Vollenweider (1968). Recently Korde (1966b) presented the rationale for proposed schemes based solely on lake sediment characteristics. The strength of a lake classification scheme based on sediment analyses lies in the ability to interpret and compare past and present states. Classifications based on single indicator organisms are weak, due chiefly to inadequate knowledge of species autecologies and nutritional physiology. A scheme based not on single diatom species but groups, namely Centrales and Araphidineae, is not subject to these inadequacies and the rationale for its use has previously been discussed in detail (Stockner and Benson 1967).

Based on this classification scheme, the majority of the ELA lakes can be classified as oligotrophic. Further evidence of their oligotrophic nature is provided by studies of phytoplankton and primary production (Schindler and Holmgren 1971), zoobenthos (Hamilton 1971), periphyton (Stockner and Armstrong 1971), and water chemistry (Armstrong and Schindler 1971).

TABLE 5. A/C ratio in near-surface sediment in ELA lakes and other selected lakes at temperate latitudes in other lake districts. Scale A/C ratio: 0–1.0 oligotrophic, 1.0–2.0 mesotrophic, >2.0 eutrophic.

	A/C ratio
ELA lakes	
161	0.07
230	0.32
227	0.32
239	0.33
240	0.34
305	0.36
132	0.36
122	0.36
302	0.37
265	0.42
114	0.60
261	0.63
303	0.65
304	0.72
120[a]	1.27
241[a]	1.33
English Lake District	
Windermere, South Basin	
(avg 0–20 cm)	1.73
(avg 20–100 cm)	0.27
Windermere, North Basin	
(avg 0–20 cm)	1.01
Esthwaite Water	
(avg 0–20 cm)	2.28
(avg 20–100 cm)	0.45
Ennerdale	
(avg 0–22 cm)	0.22
Wastwater	
(avg 0–26 cm)	0.09
Seattle, Washington	
Lake Washington	
(avg 0–10 cm)	2.02
(avg 10–30 cm)	0.77
(avg 30–50 cm)	0.29
Northern Man.–Sask.	
Reindeer Lake	
(avg 0–20 cm)	0.22

[a]Meromictic.

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Chemistry of Surface Sediments of Sixteen Lakes in the Experimental Lakes Area, Northwestern Ontario[1]

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Brunskill, G. J., D. Povoledo, B. W. Graham, and M. P. Stainton. 1971. Chemistry of surface sediments of sixteen lakes in the Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Bd. Canada 28: 277–294.

This paper contains some descriptive chemical data on bedrock, soils, and profundal lake sediments of the Experimental Lakes Area (ELA). The acid granodiorite bedrock and the plagioclase–K-feldspar–quartz glacial drift of the region exhibit low rates of chemical weathering. Terrestrial vegetation, soil organic matter, and the fine fraction of the glacial drift are concentrated in the lake sediments. The major minerals of the lake sediments are quartz, plagioclase, K-feldspar, illite, chlorite, kaolinite. Loss on ignition for the lake sediment samples varies from 18 to 62% dry weight, organic carbon from 8 to 34% dry weight, total nitrogen from 0.9 to 3.5% dry weight, and total phosphorus from 0.1 to 0.3% dry weight. These surficial lake sediment samples are 88–96% water, and concentrations of major ions in sediment interstitial water are 1.5–5 times the concentration of major ions in lake water.

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The purpose of this paper is to present some chemical data on sediments of lakes in the Experimental Lakes Area (ELA) that are being studied at present. A comparison of sedimentary data from 16 of these Precambrian Shield lakes with similar data from better known lakes of the world is given.

Methods

Samples of surficial sediments were taken in early February 1969 at or near maximum depth of each lake with a tall (15 × 15 × 27 cm) Ekman dredge. Samples were accepted only when there was water above the sediment surface in the dredge. This water was gently poured out of the dredge. In general, the dredge brought up a 20–22-cm column of sediment, which represents an estimated 200–600 years accumulation. The watery mud was poured into wide-mouthed plastic bottles that were completely filled with sediment and capped tightly so that there was no air space above the sediment. Samples were rapidly transported to a field laboratory refrigerator maintained at 5 C. The samples were not frozen, since earlier results had shown that freezing altered the partitioning of elements between liquid and solid phases of the sediment.

Samples of ELA soils were collected from several profiles observed in fresh road excavations and shoveled trenches. Samples from various horizons of the profiles were spooned into plastic bags and refrigerated.

Interstitial water was extracted from sediment samples using an apparatus modified from the design of Reeburgh (1967) and Siever (1962). Wet sediments were squeezed under 20–80 psi for 2–4 hr at room temperature (20–22 C). According to Bischoff et al. (1970), warming of sediment samples from in situ temperatures ($\leq$ 4 C) to room temperature will alter ion exchange selectivity of the sediments, resulting in some enrichment of K and Cl and depletion of Ca and Mg in the liquid phase. We have not checked this source of error in the interstitial water extraction procedure. The expressed sediment water was filtered through a Whatman No. 42 filter mounted above the outlet of the sediment squeezer: solutes and colloids passing through this filter were arbitrarily designated as being "in interstitial water solution." In reality, some of the iron, manganese, aluminium, phosphorus, and silicon reported for interstitial waters in this paper were probably in particulate form.

With the exception of *p*H, Eh, and pCO_2, the chemistry of the sediment interstitial waters was not significantly altered by a 2-week storage period in a plastic bottle in a refrigerator at 4 C, compared with chemical determinations made on the day of collection. Iron, manganese, and probably some of the phosphorus precipitated in the filtrate upon exposure to atmosphere, but these elements were brought into solution by acidification. Interstitial water *p*H was measured with a Radiometer PHM 4 meter and a combination calomel-glass electrode in samples freshly squeezed from the sediment. Eh was measured at the same time with a 1 N HCl cleaned platinum-calomel electrode pair. The potential difference obtained was added to the potential of the calomel

[1]The thirteenth in a series of 14 papers on the work of the Fisheries Research Board of Canada, describing background environmental data on the Experimental Lakes Area, northwestern Ontario. For location of numbered lakes see insert map at the back of this issue of the Journal of the Fisheries Research Board of Canada. A key to lake locations is given by Cleugh and Hauser (1971).

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electrode relative to the standard hydrogen electrode. Samples for major ions and nutrient elements were kept in a refrigerator until analysis.

Water content of the sediment was determined by loss of weight upon drying at 110 C and the ash by ignition of these samples at 900 C for 6–8 hr. Iron, manganese, aluminium, and phosphorus were extracted from some 110 C dried samples with 1 N HCl, or $Na_2S_2O_4$ – 1 M $NaHCO_3$ – 0.3 M Na–citrate, following the procedure of Jackson (1968). Fe and Al were determined spectrophotometrically in these previously described extracts by methods outlined in Sandell (1965). Ashed samples of rock, soil, or total sediment (solid and liquid phase) were fused in HF–HCl (Pawluk 1967) for measurement of Ca, Mg, Na, K, total Fe, total Mn, total Al, and Ti by atomic absorption spectrophotometry (Perkin-Elmer 303). Atomic absorption spectrophotometric standards were prepared by adding standard solutions to fused sediment samples, and from fusion of U.S.G.S. rock standard G-2 (Flannagan 1969). Lanthanum was added as an interference suppressor in the determination of Ca and Mg. Triplicate atomic absorption determinations were made on all fused samples; Table 1 gives standard deviations from the mean of analyses of U.S.G.S. standard rock fusions. A separate NaOH fusion (Shapiro and Brannock 1956) was prepared for colorometric measurement of Si (Armstrong and Butler 1962).

Conductivity was measured with a YSI conductance bridge at 1 KHz calibrated against standard KCl solutions. Chloride was measured according to APHA Standard Methods (1965) by volumetric $Hg(NO_3)_2$ titration. Sulfate was precipitated with barium and gravimetrically determined (APHA Standard Methods 1965). Total dissolved nitrogen and total dissolved phosphorus in interstitial waters were determined after photochemical combustion (Armstrong and Tibbitts 1968) according to the methods of Wood et al. (1967) and Murphy and Riley (1962). The method of Murphy and Riley (1962) was also used to determine ΣP in the fusion solution. A separate low temperature (500 C) ashing, bisulfate fusion, and HCl–HF extraction was done to check for possible loss of P by volatilization. This low temperature procedure gave P values nearly identical to values obtained from the Pawluk (1967) procedure.

Sediment samples from lakes 120, 227, 239, 241, and a sample of pink granodiorite from the lake 239

TABLE 1. Chemical relation of ELA sediments to U.S.G.S. standard rock, crustal abundances, and other analyses of Precambrian Shield rock, expressed as % of ash weight.

	G-2[a]	G-2[b]	Crustal abundance[c]	Red L., Ont., Precambrian Shield[d]	Avg Canadian Precambrian Shield[d]	ELA bedrock (L. 239)	ELA mean surface sediment composition[e]
Ca	1.42	1.15±0.05	2.96	2.84	2.94	0.98±0.060	0.99±0.28
Mg	0.47	0.49±0.007	1.87	1.24	1.35	0.30±0.019	0.47±0.16
Na	3.08	2.96±0.24	2.50	2.87	2.57	3.57±0.006	0.62±0.37
K	3.74	3.39±0.27	2.50	1.87	2.57	2.57±0.068	0.88±0.38
Fe	1.87	1.99±0.02	4.65	3.10	3.09	0.80±0.008	4.15±2.2
Mn	0.02	0.03±0.000	0.10	0.05	0.053	0.02±0.000	0.09±0.07
Al	8.12	8.87±0.29	8.04	8.13	7.75	8.35±0.26	7.4±1.6
Si	32.34	32.12±2.22	29.5	30.99	30.3	33.70±5.48	35.4±3.7
Ti	0.32	0.43±0.01	0.45	0.28	0.31	0.11±0.003	0.31±0.07
P	0.06	0.09±0.006	0.09	0.06	0.065	0.05±0.002	0.41±0.15
Li			–	0.002	0.0022	0.023	0.021±0.005
Ni			0.0058	0.002	0.0023	0.002	0.009±0.003
Cr			0.0083	0.0054	–	Trace	0.013±0.011
Zn			–	–	–	0.005	0.007±0.001
Co			0.0018	0.0012	0.0021	0.013	0.007±0.004
S	0.02		0.05	0.03	0.06	0.003	
Cl	0.02		0.02	0.01	0.01	–	
F	0.13		0.07	0.03	0.05	–	
Sr	0.04		0.034	0.052	0.034	–	
Cu			0.047	0.0017	0.0014	–	
Ba	0.16		0.065	0.065	0.11	–	
V			0.0090	0.0068	0.0053	–	

[a]Average of analyses by 29 laboratories of G-2 given by Flanagan (1969).
[b]Analyses of G-2 samples by our laboratory.
[c]Vinogradov (1962).
[d]Shaw et al. (1967).
[e]Mean values from Table 4.

watershed were analyzed for all elements in ash reported here by one of us (M.P.S.) with E. E. Angino at the University of Kansas geochemical laboratories. These separate analyses served as an outside check on our methods.

A Philips X-ray diffractometer was used to determine the major minerals in the local bedrock, soils, and lake sediments. Diffractograms were made with Fe filtered, Co radiation at 36 Kv and 10 mA. Samples were scanned at a speed of 1° 2Θ per minute with a 1° divergence slit, 0.1 mm receiving slit, and a 1° scatter slit for 2–40° 2Θ, and a 4° divergence slit, 0.2 mm receiving slit, and 4° scatter slit for 32–60° 2Θ. Sediment, soil, and rock samples, dried at 110 C and ground to a powder, were packed in a Philips aluminum sample holder for preliminary determinations of mineralogy. Particle size separations were made with a Sorval centrifuge on a few lake sediments and soils according to techniques of Jackson (1968). Coarse, medium, and fine silt, and the coarse and fine clay fractions were saturated with Mg–glycerol and with K for clay mineral determination. The K-saturated fractions were heated to 300 and 550 C and again subjected to X-ray diffraction analyses to determine expandible lattice minerals.

A dry combustion method was used to determine total carbon, total nitrogen, and hydrogen using a Perkin-Elmer model 240 Elemental Analyzer. Prior to analyses samples were dried at 110 C, homogenized by grinding to powder in a mortar with a pestle, then dried again overnight at 105 C. The instrument was calibrated with acetanilide. No addition of oxidant was attempted. The coefficient of variation for replicate calibrations was 0.27% for N, 0.22% for C, and 0.63% for H. Average deviation from the mean of duplicate analyses of lake sediment samples was 0.33% for C, 1.14% for N, and 0.92% for H. Since we found no carbonate minerals in these profundal sediments, total carbon (ΣC) was interpreted as organic carbon. Sedimentary chlorophyll extractions were made according to the methods of Vallentyne (1955). Freeze-dried, oven-dried, and fresh wet sediment samples were extracted. The spectrum of the extract was recorded on a Cary 14 spectrophotometer.

Results

Local Bedrock and Glacial Till Deposits

Reconnaissance geologic mapping of bedrock in the Rainy River–Kenora district by Davies and Watowich (1958) and Davies and Pryslak (1967) indicated that ELA drainage basins are in an area of predominantly pink granodiorite. Localized zones of biotite-rich granodiorite occur as darker colored outcrops in several localities.

The chemical composition of a sample of a surface outcrop of the pink granodiorite bedrock from the drainage basin of lake 239 is given in Table 1. In comparison to Vinogradov's (1962) estimate of crustal abundance and some estimates of mean composition of the Canadian Pre-Cambrian Shield (Shaw et al. 1967), the local bedrock sample was low in Ca, Mg, Fe, Mn, and Ti, and enriched in Na, Al, and Si (Table 1). This is consistent with Davies and Watowich's (1958) data and our X-ray diffraction data that indicate that quartz, plagioclase, K-feldspar, and muscovite are the major minerals of the lake 239 bedrock (Table 2). Table 1 also gives values for some trace elements in Shield areas and is an indication of the order of magnitude to expect for these elements in ELA bedrock. Glacial drift of the area is extremely variable in thickness, extent, and particle-size composition, but sands and gravel of quartz, plagioclase, and K-feldspar predominate (Dell 1963).

Soils

Our incomplete knowledge of ELA soil types was summarized by Brunskill and Schindler (1971). In areas of till and glaciofluvial gravels, immature brunisols were observed similar to the lake 468 (Roddy Lake) exposure described in table 2 and fig. 3*a* in Brunskill and Schindler (1971). Most ELA soils were less well defined and much thinner than the lake 468 profile. Other soil types were found but have not been sampled in detail (Table 3). In some valleys, glaciolacustrine or alluvial deposits, or both, occur, and water-saturated gleysols developed in these areas. Most of these soils developed over plagioclase and quartz sand, with <10% silt and clay. The clay minerals were a rather complex mixture of kaolinite, interstratified illites, chlorite, and perhaps some montmorillonite of poor crystallinity. Surface runoff, soil interstitial water, and soil–water slurries of the surface horizon (L–H) of most soils in the area had *p*H values in the range 4–5 and were usually yellow-brown in color.

Lake Sediments

The solid phase

The inorganic chemical composition of surficial sediment samples of 16 lakes in ELA is given in Table 4. Si, Al, and Fe were the most abundant elements, and in their oxide form comprise nearly 50% of the total dry sediment. These elements were found mostly in the abiogenic fraction of the sediments, i.e., the minerals quartz, plagioclase, and K-feldspars (Table 2). Si was directly correlated to ash content of the lake sediment samples, but Al, Ca, Mg, Na, K, Fe, and Mn did not appear to be related to ash content (Table 4). Phosphorus was inversely related to ash content (Fig. 1), and less clearly related to Fe in the ash of these lake

TABLE 2. Mineralogy and particle size data for lake 239 bedrock, ELA soils, and lakes 239, 230, and 241 profundal sediments (0–20 cm sediment depth).

Sample		Size fraction	Inorganic fraction %	Dry wt %	Major minerals	Minor minerals
L. 239 bedrock		–	–	–	Quartz (40%), plagioclase (40%), K-feldspar (10%)	Ilmenite (1%), kaolinite (tr), muscovite (5%)
L. 468 soil profile	LF	Total			Organic matter	–
	Ae	Sand (>50 μ)	–	99	Plagioclase, quartz	
		Silt & clay (<50 μ)	–	1	Plagioclase, quartz, chlorite, illite	Kaolinite, ?montmorillonite, interstratified clays
	Bf	Sand	–	99.5	Quartz, plagioclase	Magnetite
		Silt & clay	–	0.2	Chlorite, illite	
	C	Pebble & sand	–	100	Quartz, plagioclase, chlorite	Biotite
L. 239 sediments (0–20 cm)		Sand (>50 μ)	3	1.4	Quartz, plagioclase, K-feldspar	
		Silt (2–50 μ)	47	20	Quartz, plagioclase, K-feldspar	Illite, chlorite, kaolinite
		Clays (<2 μ)	50	21	Illite	Quartz, plagioclase, K-feldspar, chlorite, kaolinite, montmorillonite
L. 230 sediments		Sand	8	3	Quartz, plagioclase, K-feldspar	
		Silt	78	24	Quartz, plagioclase, illite	Chlorite, quartz
		Clay	13	4	Illite, kaolinite	Chlorite
L. 241 sediments		Sand	17	6	Quartz, plagioclase, K-feldspar	
		Silt	73	23	Quartz, plagioclase, illite	
		Clay	10	3	Quartz, K-feldspar, illite, kaolinite	

TABLE 3. General characteristics of ELA soils.

Locality	Type	Horizon	Color	*p*H[a]	Loss on ignition at 900 C % dry wt	% ΣC dry wt	% ΣN dry wt
L. 468 (Roddy L.) landing near ELA road	Brunisol	LF	Brown-black	4.5	81	41.5	1.7
		Ae	Light grey	6.0	2.0	0.9	0.35
		B	Tan-brown	5.0	0.5	–	–
		C	Tan to pink-rust	–	0.0	–	–
L. 239 E Inlet valley	Gleysol on alluvial deposits	A	Black	6.5–7.0	10	–	–
S of L. 228 (Teggau L.) trail	Brunisol	B	Red-rust	4.0	7.2	–	–

[a]Soil *p*H was measured in a slurry of equal volumes of soil and distilled water (see Jackson 1968).

TABLE 4. Chemical composition of ash of surface (0–20 cm) sediments from the profundal zone of selected ELA lakes, expressed as % of ash weight.

Lake:	161	305	239	265	240	302N[a]	230	122	261	227	304	132	303	114	241	120
Ca	1.17	1.09	0.66	0.89	0.82	1.23	1.05	0.79	0.64	1.31	0.72	0.64	1.20	1.23	1.59	0.87
Mg	0.67	0.77	0.42	0.42	0.52	0.74	0.54	0.35	0.30	0.25	0.37	0.47	0.54	0.49	0.42	0.28
Na	–[b]	1.21	0.32	0.39	0.78	1.52	0.53	–	0.31	0.30	0.47	0.53	0.70	–	0.52	0.48
K	1.48	1.38	0.49	0.69	1.00	1.73	0.95	0.77	0.50	0.38	0.71	0.94	0.99	0.91	0.66	0.54
Fe	2.99	4.30	4.41	5.35	3.48	2.61	5.80	1.45	1.55	9.03	3.42	2.81	2.64	3.00	8.72	4.91
Mn	0.21	0.16	0.05	0.25	0.06	0.05	0.19	0.02	0.02	0.15	0.05	0.05	0.03	0.02	0.05	0.12
Al	6.7	8.6	5.3	8.6	7.1	8.0	7.4	6.6	5.4	9.0	5.8	7.2	6.8	6.9	12.0	7.2
Si	32.2	35.2	33.5	34.2	40.1	39.6	34.2	29.2	42.5	31.8	38.0	36.7	37.9	34.5	30.1	36.2
Ti	–	0.42	0.26	0.30	0.30	0.41	0.36	–	0.22	0.22	0.29	0.31	0.34	–	0.40	0.22
P	0.33	0.28	0.32	0.58	0.24	0.20	0.66	0.33	0.26	0.59	0.39	0.51	0.58	0.31	0.60	0.39
Li	–	–	0.024	–	–	–	–	–	–	ND[c]	–	–	–	–	ND	0.017
Ni	–	–	0.005	–	–	–	–	–	–	0.013	–	–	–	–	0.012	0.007
Cr	–	–	0.0009	–	–	–	–	–	–	0.018	–	–	–	–	0.026	0.008
Zn	–	–	0.008	–	–	–	–	–	–	0.008	–	–	–	–	0.007	0.006
Co	–	–	0.004	–	–	–	–	–	–	0.013	–	–	–	–	0.006	0.005
% ash of dry wt	81.9	76.0	68.5	56.5	70.2	68.3	37.6	59.8	58.0	44.3	49.3	51.2	41.6	41.5	40.6	57.9

[a]302N = lake 302, north basin.
[b]Dash (–) indicates not measured.
[c]ND = not detected.

sediment samples (Fig. 2). The range of variation for most elements (other than Si and Al) shown in Table 4 was considerable (generally a factor of 3–5), in spite of the presumed homogeneity of the drainage areas (Brunskill and Schindler 1971). Maximum variation was found within the Na, K, and Mn data, and molal ratios indicated fluctuations in Si:K, Si:Na, Si:Ca, Si:Mg, Fe:Mn, and Al:P (Table 5). Since the inorganic fraction of these sediments was predominantly composed of a few silicate minerals, we might expect rather constant ratios of Si to other elements. However, these ratios may be more influenced by variation in the abundance of quartz than by variation of ratios of feldspar or clay mineral cations. Fe and Mn concentrations in the sediments were expected to show some relation to Eh or O_2 depletion in lake hypolimnia (or monimolimnia) (see Schindler 1971a) but no consistent relation was found (Tables 4, 5, and 7). Molal ratios of Si:Al average near 3, the values expected for most feldspars and their decomposition products. Variation in Na:Ca, Na:K, and Ca:Mg was controlled to a mean of 1.1–1.4 (Table 5). Variation of Fe:P was small compared with other ion ratios, and may be examined in more detail in Fig. 2.

Some particle size distribution data for these sediment samples are shown in Table 2. Nearly

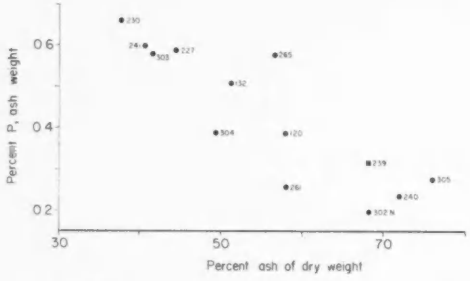

FIG. 1. Relation between P (% ash weight) and ash (% dry weight) for surface samples of profundal sediments of selected ELA lakes. Lake numbers are shown by each point.

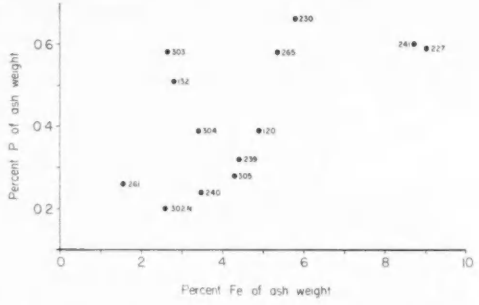

FIG. 2. Relation between P (% ash weight) and Fe (% ash weight) for surface samples of profundal sediments of selected ELA lakes.

TABLE 5. Molal ratios (on a 110 C oven-dry weight basis) for sediment chemical data of ELA. These values are derived from Table 4.

Lake	Si:Al	Si:K	Si:Na	Si:Ca	Si:Mg	Fe:Mn	Na:Ca	Na:Mg	Na:K	Ca:Mg	Fe:P	Al:P
161	4.1	27	–	35	37	9	–	–	–	1.1	4.70	21
305	3.9	36	24	46	39	27	1.9	1.7	1.5	0.85	8.48	35
239	6.1	95	86	74	69	87	0.85	8.1	1.1	0.94	7.56	19
265	3.8	69	72	55	70	21	0.77	9.8	0.96	1.3	4.91	16
240	5.4	56	42	69	68	6	1.7	1.6	1.3	0.98	8.07	34
302N	4.8	32	21	46	46	51	2.2	2.2	1.5	1.0	7.23	46
230	2.7	50	53	47	56	30	0.90	1.0	0.95	1.2	4.88	21
122	4.3	53	–	53	73	60	–	–	–	1.4	2.40	22
261	7.6	118	112	95	125	74	0.85	1.1	1.1	1.3	3.29	24
227	3.4	118	90	35	112	60	0.39	1.3	1.3	3.2	8.52	18
304	6.1	74	67	77	90	66	1.2	1.4	1.1	1.2	4.87	18
132	4.9	55	57	82	68	54	1.4	1.2	0.96	0.83	3.06	16
303	5.4	54	45	45	63	90	1.0	1.4	1.2	1.4	2.38	13
114	4.0	44	–	34	51	149	–	–	–	1.5	5.30	25
241	2.4	63	48	27	62	158	0.56	1.3	1.3	2.3	8.11	23
120	4.8	95	61	60	113	41	0.98	1.8	1.5	1.9	6.96	21
$\bar{x}$	4.6	65	60	55	71	61	1.1	2.6	1.2	1.4	5.67	23
$S_{\bar{x}}$	1.3	28	26	20	26	44	1.2	2.9	0.2	0.62	2.2	8.4

50% of the inorganic fraction of lake 239 profundal sediment is of clay size (<2 μ). Sand-sized grains were almost entirely quartz and feldspars, with some chlorite. Quartz and feldspars were found even in the fine-grained sediments, but kaolinite, illite (or hydrated mica), and chlorite were more abundant. Some indication of the presence of trace amounts of poorly crystallized montmorillonite was found. Montmorillonite would not be expected to form or to be stable in local soils or lake waters of such low ionic strength. An alternate source of this mineral was found in dry fallout collected with accumulated snow from the surface of lake 132 (Table 6). Well-crystallized montmorillonite was a major component of this atmospheric sediment. Subsequent collections from other lakes in winter 1969–70 yielded samples with little or no clay material (J. Barica, personal communication). In lakes 230 and 241, the silt (2–50 μ) fraction predominated in the profundal lake sediment but the mineral assemblages were similar to sediments of lake 239.

Table 7 gives data on the biophilic elements carbon and nitrogen in these profundal ELA sediment samples. Percentage weight loss on ignition (L.O.I.) was found to relate rather well to total carbon (ΣC) in these lake sediment samples. The ratio L.O.I.:C was about 2.7 in ELA lake sediments low in organic material, and was about 2.3 in lakes high in organic material. There was a linear relation between ΣC and ΣN in different lake sediments, but sediment samples from lakes 303 and 132 were enriched in ΣN. The molal ratio C:N did not change significantly with increasing C content in the sediment. The water-sorptive property of sediments rich in organic material is demonstrated in Table 7. The disparity between ΣN and Kjeldahl N shown in Table 7 may be due to incomplete conversion of organic N to NH_3 and sorption of N species to clay-sized particles in the sediments. Special efforts were made to ensure minimal postsampling atmospheric contamination. At present, the source of discrepancy in the N data is poorly known (Bremmer 1965). Phosphorus concentrations remained relatively unaffected by increasing carbon content; because of this, the ratio N:P increases with increasing organic carbon in these lake sediment samples. Table 8 indicates the variation of water content and weight loss on ignition in surface sediment samples at different depths within two ELA lake basins. Shallow areas in most of these lakes usually have coarse sandy sediments with pebbles or boulders, or both, similar to lake sediment distribution described by Frink (1969) and Delfino et al. (1969).

Chlorophyll concentrations in these profundal sediment samples varied considerably (Table 7). With the exception of the very shallow lakes 114 and 303, sedimentary chlorophyll concentrations increased with increasing ΣC and preliminary estimates of primary production (per cubic meter) (Schindler and Holmgren 1971; Schindler 1971c). In general, more chlorophyll was extracted from freeze-dried sediment than from oven-dried sediment, and extraction from wet sediments yielded less pigment than either of these previous methods. The data in Table 7 on chlorophyll concentrations in these sediment samples must be regarded as preliminary.

The water phase

The chemical composition of water squeezed from profundal sediments of ELA lakes is given in Table 9. Our sediment–water extraction procedure obtained about 20–30% of total water content (as determined by drying to 110 C, Table 9). Freshly extracted interstitial water ranged in color from clear to yellow-brown, and had the odor of rotten wet wood. Shortly after extraction, Fe, Mn, and probably other elements began to precipitate. Interstitial water *p*H ranged from 6.2

TABLE 6. Particle size and mineralogical composition of particulate material in accumulated snow from lake 132, late winter 1968. Sample provided by F. A. J. Armstrong.

Size fraction	% of ash	% of dry wt (110 C)	% loss on ignition of dry wt	Minerals in order of decreasing abundance
Sand (>50 μ)	4.7	3.2	32.5	Montmorillonite
Silt (2–50 μ)	72.7	49.1		Illite
				Chlorite
Clay (<2 μ)	22.6	15.2		Kaolinite
				Quartz
				Plagioclase

TABLE 7. Loss of weight after ignition at 900 C (L.O.I.), total carbon (ΣC), total nitrogen (ΣN), Kjeldahl nitrogen (N_k), total phosphorus (ΣP), expressed as percent of 110 C dry sediment weight, for profundal sediment samples (homogenized, 0–20 cm sediment depth) from selected ELA lakes. Water content (% H_2O) is expressed as percentage loss of weight of wet sample after drying to 110 C. Ratios are on a molal basis. One standard deviation is given in parentheses in the lake average column, and the deviation for lake 227 is for three separate dredge samples. Sedimentary chlorophyll degradation products (SCDP) are calculated according to Vallentyne (1955) after three methods of extraction: (1) 90% acetone extraction of 110 C oven-dried sediment, (2) extraction of freeze-dried sediment, and (3) extraction of wet sediment.

Lake:	161	305	239	265	240	302N	230	122	261	227	304	132	114	303	241	120	Avg of 16 lakes
% H_2O	88.1	89.9	90.7	95.4	91.9	94.6	96.9	93.8	95.8	95.8±0.6	96.8	95.9	96.2	96.2	95.8	94.5	94.3±2.7
L.O.I.	18.1	24.0	31.5	43.5	29.8	31.7	62.4	40.2	42.1	48.5±0.09	50.7	48.8	58.5	58.4	59.4	42.1	43.6±14
ΣC	8.0	10.7	13.6	20.6	14.0	15.3	33.6	19.3	22.7	23.0±1.0	25.1	24.0	28.1	28.2	20.1	20.2	20.4±7
ΣN	0.90	1.08	1.37	2.12	1.44	1.92	3.04	1.6	2.14	1.7±0.17	2.41	3.33	2.4	3.51	2.52	1.81	2.1±0.76
N_k	–	0.77	1.06	1.56	1.13	1.32	2.70	–	2.02	1.91	2.26	2.21	–	2.68	2.11	1.69	1.80±0.61
ΣC:ΣN	10.4	11.6	11.6	11.4	11.3	9.3	12.9	14.1	12.3	13.4	12.2	8.4	13.7	9.4	13.9	13.0	11.8±1.7
ΣN:ΣP	8.2	11.2	13.8	13.7	19.1	31.1	27.1	22.0	31.1	19.9	27.7	28.2	34	32.2	23.1	17.7	22.5±8.1
ΣC:ΣP	77	129	159	156	215	290	350	243	385	266	338	238	554	301	322	231	266±115
SCDP (1)	–	20	170	190	200	230	770	–	910	330	530	930	–	140	900	220	–
(2)	–	30	210	350	200	240	1440	–	890	–	350	1000	–	240	–	–	–
(3)	6	5	70	120	94	160	770	420	450	350	560	320	60	140	420	180	–

to 7.3, which was generally equal to or greater than the *p*H of overlying lake water. Eh measurements taken within 2–6 hr of collection time usually stabilized in 5 min to values above +200 mV in interstitial waters of holomictic lakes; interstitial waters of ELA meromictic lakes (241, 120) were from −80 to −160 mV according to field laboratory measurements. In situ Eh measurements (using a Pt-calomel electrode pair on 50-m leads) in lake 241 sediments gave values from −180 to −230 mV.

Interstitial waters from profundal sediments of ELA holomictic lakes had greater concentrations of dissolved ions than the overlying lake water (Table 10). The variation observed in interstitial water:lake water ion ratios for different holomictic lakes was considerable and did not appear to be related to our present knowledge of differences in the composition of the sediments. Waters of holomictic lakes had nearly equimolar concentrations of Ca and Na (Armstrong and Schindler 1971), and interstitial waters had a mean molar Ca:Na ratio of 2.6 (Table 9). In general, Fe and Si were greatly enriched in sediment interstitial water compared with lake water (Table 10).

In meromictic lakes 120 and 241, where profundal sediments have been in contact with monimolimnetic water for long periods of time, interstitial water and monimolimnetic water were very similar in chemical composition. Higher concentrations of dissolved Fe in monimolimnia are the result of negative redox potentials (Table 9); lower concentrations of Fe in interstitial waters may indicate an approach to equilibrium with some ferrous mineral in the sediments, or diffusion of Fe^{++} from the sediments to monimolimnetic water.

TABLE 8. Variation of water content (% H_2O) and loss of weight on ignition (L.O.I.) for several samples of surface sediments from two ELA lakes. Localities are given in coordinates from bathymetric charts given by Brunskill and Schindler (1971).

Location	Water depth	% H_2O of wet wt	% L.O.I. of dry wt
	Lake 239		
C.0–10.0	4.5	73.4	11.1
B.5–3.0 (0–10 cm)	9	89.6	30.2
B.5–3.0 (10–20 cm)	9	90.6	30.2
D.7–3.6 (0–10 cm)	15	91.2	28.7
D.7–3.6 (10–20 cm)	15	79.8	12.8
I.3–3.0	7	54.6	2.9
J.0–6.5	9	89.0	28.2
F.5–4.5	31	90.7	24.0
	Lake 230		
F.0–3.7	5	97.8	61.7
G.0–7.0	9.5	97.4	46.6
G.0–9.8	9.5	96.9	55.8
G.0–8.0	13.0	96.9	62.4

Discussion

The solid phase of sediments of ELA lakes was composed chiefly of watershed soils, silts, and clays derived from glacial drift that were physically transported to the lake by surface runoff. Glacial drift originated from the northwest, north, and northeast of ELA and was derived primarily from Precambrian Shield regolith. This material, of heterogeneous composition and particle size, was reworked and eroded by at least two glacial lakes. Several climatic and vegetational regimes exerted an influence upon glacial drift weathering and soil formation in ELA (Brunskill and Schindler 1971). In addition, suspended sediments from the west were brought into some areas of northwestern Ontario by glacial Lake Agassiz (Elson 1967). The fact that the lake sediments are low in concentrations of Ca (Table 1) indicates that little or none of the Ca-rich Agassiz sediments reached ELA.

The soils of ELA obviously are not "residual soils" and would not be expected to be closely related to underlying bedrock, as in the case described by Harriss and Adams (1966). However, our preliminary observations indicate that most glacial drift and B horizon soils are similar mineralogically to lake 239 bedrock (Table 2). Due to greater surface area, sands, silts, and clays of glacial drift are far more reactive to leaching soil–water solutions than the bedrock. This fine fraction of glacial drift is delivered to the lake in two forms: (*a*) as ions, molecules, inorganic or organic complexes in solution; and (*b*) by physical transport of unaltered minerals and insoluble residues of solution phenomena mentioned above. The lakes concentrate the fine fraction of soils and glacial drift very efficiently (Table 2), but with very little change in mineralogical composition.

In the ELA environment the major reactions of weathering in soils and lake water should be hydrolysis:

$$[Na, K, Ca, Mg]\ \text{Alumino-silicate} + CO_2 + H_2O \rightarrow \text{insoluble residue} + H_4SiO_4 + [Na + K + Ca + Mg] + HCO_3. \quad (1)$$

This reaction (equation 1) proceeds very slowly, and the insoluble residue from an initial reaction may go through several stages of decomposition with continued exposure to leaching solutions. According to studies by Harriss and Adams (1966) on soil

TABLE 9. Chemical composition of interstitial water squeezed from a homogenized surface (0–20 cm sediment depth) sample of profundal sediments from selected ELA lakes, in μmoles/liter. Samples were taken in February 1969. Standard deviation in the lake 227 column is for three separate dredge samples at the station.

Lake:	161	305	239	265	240	302N	230	122	261	227	304	132	303	114	241	120
$\%H_2O$	88.1	89.9	90.7	95.4	91.9	94.6	96.9	93.8	95.8	95.8±0.6	96.8	95.9	96.2	96.2	95.8	94.5
*p*H[a]	6.70	7.30	6.51	6.72	6.43	6.74	6.72	6.40	6.20	6.84	6.70	6.29	6.35	6.21	6.48	6.84
Eh[a] (*mV*)	–	–	+340	–	+320	–	–	–	+300	+200	–	–	–	–	–185	–100
Cond[b]	–	82	44	68	–	64	78	–	–	105	76	43	57	–	240	232
Ca	130	272	86	169	87	105	118	58	71	198±18	190	70	155	115	264	497
Mg	55	160	37	46	37	26	36	24	35	39±1.5	42	17	44	60	70	61
Na	69	139	70	63	60	41	43	48	52	65±8.4	38	31	35	55	89	90
K	32	43	20	19	16	17	23	18	15	21±0.6	14	18	18	18	55	44
ΣFe	1	20	100	25	76	20	196	3	63	289±52	106	18	30	1	777	1990
ΣMn	10	21	4	36	9	4	17	2	4	17±3.6	5	2	3	1	9	96
Si	194	205	279	236	311	90	231	285	150	349±48	240	123	81	148	333	217
ΣAl	<40	<4	<4	<4	34(?)	<4	<4	<40	76(?)	11	<4	<4	<4	<40	<4	11
Cl	395	17	17	45	–	17	39	73	–	100±13	45	17	17	79	56	56
SO_4[b]	73	115	83	–	–	–	–	62	–	275±85	–	–	–	62	104	145
TDN[c]	–	–	10	31	–	17	60	–	–	–	64	16	15	–	69	–
TDP[c]	–	–	0.4	5	–	11	0.4	–	–	–	7	6	1	–	53	–

[a]*p*H and Eh measurements were made in a field laboratory within 4 hr of collection and immediately after squeezing for lakes 239, 240, 261, 227, 241, and 120. Other lake samples were stored up to a week before squeezing and measurement.

[b]Measurements of specific conductance (μmhos/cm at 25 C) were made on stored samples some time after squeezing, and represent conductivity *at the time of analysis* (often a week after squeezing). This qualification is especially pertinent to sediment interstitial water from lakes 241 and 120, which have in situ conductivities of ~500 and 950–1000 μmhos/cm, respectively. Data given here reflect the loss of CO_2, H_2S, NH_3, and Fe from the water sample. Some of the high SO_4 values may be due to oxidation of H_2S during storage of the sample.

[c]Due to difficulties in the photochemical combustion of these samples, total dissolved nitrogen (TDN) and total dissolved phosphorus (TDP) data are to be regarded as *minimal* values.

TABLE 10. Molar ratios of ion concentrations in interstitial waters (IW) of each lake sediment sample and each lake water (L). Values in parentheses indicate uncertainties due to small numbers of analyses.

Lake	$\frac{IW_{Ca}}{L_{Ca}}$	$\frac{IW_{Mg}}{L_{Mg}}$	$\frac{IW_{Na}}{L_{Na}}$	$\frac{IW_{K}}{L_{K}}$	$\frac{IW_{Fe}}{L_{Fe}}$	$\frac{IW_{Mn}}{L_{Mn}}$	$\frac{IW_{Si}}{L_{Si}}$
161	1.7	1.6	1.3	2.9	–	–	24
305	4.7	5.3	3.2	4.3	(200)	–	5.4
239	1.5	1.1	1.3	1.7	560	–	11.6
265	3.8	1.1	1.3	1.7	23	–	–
240	1.8	1.2	1.3	1.7	(760)	–	4.8
122	2.0	0.9	1.4	2.1	3.3	–	–
302	2.8	1.0	1.2	1.8	–	–	1.0
230	2.1	1.2	0.7	1.6	–	–	4.5
261	2.2	1.3	1.2	2.4	210	–	29
227	2.2	1.8	1.2	1.7	4.0	3.8	17
304	5.3	1.6	0.9	2.0	–	–	5.8
132	2.3	0.6	1.3	2.1	36	–	–
114	3.7	2.2	1.4	2.0	–	–	9.3
303	6.2	1.9	1.0	3.5	–	–	5.8
241	0.9	0.7	1.2	1.1	0.70	1.1	2.8
120	1.0	1.2	1.4	1.3	0.76	1.0	(1.1)

development over granite, the order of relative stability of the major minerals found in ELA soils and sediments would be plagioclase, biotite, K-feldspar, and quartz, from least to most stable respectively. Following the theory and applications of Helgeson et al. (1969), Garrels and MacKenzie (1967), and Garrels and Christ (1965), it is possible to represent this complex weathering reaction as:

$$\underset{\text{(anorthite)}}{CaAl_2Si_2O_8} + 2H^+ + H_2O \rightarrow \underset{\text{(kaolinite)}}{H_4Al_2Si_2O_9} + Ca^{++}, \quad (2)$$

$$\underset{\text{(albite)}}{2NaAlSi_3O_8} + 2H^+ + 9H_2O \rightarrow \underset{\text{(kaolinite)}}{H_4Al_2Si_2O_9} + 2Na^+ + 4H_4SiO_4, \quad (3)$$

$$\underset{\text{(K-mica)}}{2KAl_2Si_3O_{10}(OH)_2} + 2H^+ + 3H_2O \rightarrow \underset{\text{(kaolinite)}}{3H_4Al_2Si_2O_9} + 2K^+, \quad (4)$$

$$\underset{\text{(K-feldspar)}}{2KAlSi_3O_8} + 2H^+ + 9H_2O \rightarrow \underset{\text{(kaolinite)}}{H_4Al_2Si_2O_9} + 2K^+ + 4H_4SiO_4, \quad (5)$$

$$\underset{\text{(kaolinite)}}{H_4Al_2Si_2O_9} + 5H_2O \rightarrow \underset{\text{(gibbsite)}}{Al_2O_3 \cdot 3H_2O} + 2H_4SiO_4. \quad (6)$$

Minerals in ELA soils and lake sediments are more complex than this simplified formulation, i.e., plagioclase may contain varying proportions of Na and Ca, and the micas contain Na, Fe, Mg, and K. However, the progress of these reactions can be monitored or predicted by measuring H^+, Na^+, K^+, and Si concentrations in solution, assuming the activity of the solid phases and water to be unity. Using the measured values of *p*H, *p*Na, *p*K, and *p*Si for interstitial waters of the lake sediments (Table 9) in a stability diagram (see Garrels and Christ 1965) it was apparent that kaolinite was the thermodynamically stable phase in contact with water of this composition. Kaolinite was indeed found in all of the lake sediments, but illite, chlorite, interstratified clays, poorly crystallized montmorillonite, plagioclase, and K-feldspar were also found in the fine (=reactive) fraction of the lake sediments (Table 2). We can expect from equations 2–5 that these last-mentioned minerals should slowly release cations (Na, K, Ca, Mg) and Si in exchange for H^+ to form kaolinite. H^+ in these reactions comes largely from the hydration and solution of atmospheric CO_2 in soil water. Table 10 indicates that concentrations of cations in interstitial water were higher than lake water concentrations, which may indicate that reactions similar to equations 2–5 are in progress. Ohle (1955) reported similar enrichments of major ions in interstitial waters of Grosser Plöner See sediments. Table 10 also indicates that Ca was more abundant in interstitial water solutions than Na or K. It is likely that the smaller proportion of Ca in the plagioclase dissolves faster than the Na–plagioclase and K–feldspar (see Loughnan 1969 p. 13; Todd 1968). Selective leaching or chelation of certain ions by humic acids and lignins may also play a role in

the composition of the solution (Loughnan 1969; Thompson and Chesters 1969).

Kramer (1968) found a somewhat simpler suite of minerals in sediments of Precambrian Shield Lake Onaping. Soils and lake sediments derived from glacial tills in the drainage area of eutrophic Bantam Lake, Connecticut, are more mature; clay minerals of the lake watershed appeared to be altered by reaction with lake water (Fink 1969, 1965). ELA lake sediments, which are mostly allochthonous to the watershed as well as to the lake basin, do not appear to be altered greatly by percolating soil water or lake water (e.g., the persistence of unstable or metastable clay minerals). This may be due to: (*a*) low mean annual soil and sediment temperatures; (*b*) low rainfall (614 mm year^{-1}); and (*c*) the predominance of physical over chemical weathering.

In the absence of an efficient CO_2 buffering system in ELA waters equations 1–5 suggest a silicate mineral control of *p*H, as Sillén (1961) and Garrels (1965) have suggested on a larger scale. Soil water and surface runoff from ELA were usually in the *p*H range 4–6, whereas most lake surface waters and lake sediment interstitial waters were in the *p*H range 6–7.5 (Table 9; see also Armstrong and Schindler 1971).

Gibbsite was not identified in ELA sediments, and stability diagrams based on equation 6 predict that it will not form unless *p*Si decreases to less than 4.3. This is unlikely to occur in ELA (Armstrong and Schindler 1971).

The mass of dissolved ions leaving a lake and its watershed can be estimated from knowledge of the water budget and concentrations of dissolved ions in the outflow of the lake or streams flowing to the lake. The rate of weathering by solution of the land drainage area and the net loss of ions from lake water and sediments (W) was calculated as follows:

$$W_{d+l} = \frac{(\overline{M}_i)\ [(P-E)A_o + (P-E_l)A_d]}{A_o + A_d}$$

where M_i is the mean concentration of ion i in outflow waters (Armstrong unpublished data), and the other symbols are as explained and tabulated in Brunskill and Schindler (1971). Net loss of ions in solution from only land drainage areas (inflow streams) was calculated from:

$$W_d = \frac{(\overline{M}_i)\ [(P-E_l)A_d]}{A_d}$$

Some error may result from rainfall contribution, and this will be discussed later. The results of this calculation are set out in Table 11 compared with weathering rates obtained for other hard rock areas of North America. The rate of weathering in the watershed of the east inlet to lake 239 was

TABLE 11. Preliminary estimate of rates of weathering by solution (W in kg or moles ha^{-1} year^{-1}) from (*a*) terrestrial drainage areas, and (*b*) drainage areas including land and lakes, for ELA lakes 239 and 240 (1969), compared with weathering rates from Hubbard Brook watersheds in New Hampshire, USA,[a] and Clear Lake, eastern Ontario[b].

Terrestrial drainage area:	Lake 239 NW inlet		Lake 239 E inlet		Hubbard Brook[a]		Clear Lake[b]	
	kg ha^{-1} year^{-1}	moles ha^{-1} year^{-1}	kg ha^{-1} year^{-1}	moles ha^{-1} year^{-1}	kg ha^{-1} year^{-1}	moles ha^{-1} year^{-1}	kg ha^{-1} year^{-1}	moles ha^{-1} year^{-1}
Ca	1.4	34	2.6	64	10.6	264	4.5	112
Mg	0.61	25	1.0	41	2.5	104	1.3	53
Na	0.86	37	1.5	67	6.1	265	2.4	104
K	0.22	5.6	0.60	15	1.5	38	1.1	28
Si	–	–	–	–	–	–	6.4	228
Land & lake watershed:	**Lake 239**		**Lake 240**				**Clear Lake**	
Ca	1.9	48	1.6	39			3.4	85
Mg	0.73	30	0.63	26			1.1	45
Na	1.0	45	1.1	46			0.46	20
K	0.46	12	0.36	9.2			0.23	5.9
Si	1.4	49	1.8	63			0.85	30

[a]Johnson et al. 1968, 1969.
[b]Schindler and Nighswander 1970.

nearly twice the weathering rate of the northwest inlet. We do not have adequate knowledge of the variation in soils and glacial drift of these areas to account for these differences. The results for lake 239 and 240 indicate that nearly equimolar amounts of Ca, Na, and Si are being removed from the drainage area. Examination of equations 2–5 indicates that Si:Na should be 2 or greater. This Si depletion may be partly the result of biological retention of Si in the form of *Equisetum* in the drainage area and diatom frustules in lake sediments. Higher rates of chemical weathering in the New Hampshire watersheds (of similar bedrock and glacial drift composition) may be due to more rainfall and longer periods of warm weather compared with the ELA climate (see Johnson et al. 1968). Ca and Mg are higher, but Na, K, and Si weathering rates are lower in the eastern Ontario granitic watershed and lake described by Schindler and Nighswander (1970): rates of weathering by solution of the land in this area are greater than in ELA.

Another means of estimating loss of major ions from the lake drainage system is to compare the unweathered source materials of dissolved ions with the presumably leached lake sediments (Harriss and Adams 1966; Loughnan 1969). This has been done from Table 1 (using lake 239 bedrock as unweathered source material) and Table 4 (using ash of lake 239 sediments as a leached sediment). This computation reveals that relative mobility of ions is as follows (in order of decreasing mobility): $Na > K > Ca > Si \simeq Al > Mg$. By the same means, the following elements are concentrated in lake sediment ash compared to the bedrock (in order of decreasing concentration): $P \simeq Fe > Mn > Ti > Mg$. Much of the P in sediments probably comes from the atmosphere in rain and dry fallout (Armstrong and Schindler 1971).

There is a basic conflict in the above reasoning: (*a*) equations 2–5 and the ion mobility calculation suggest that Na and perhaps K should be the predominant cations released by weathering; and (*b*) calculations of weathering by solution (Table 11), the interstitial water data (Tables 9 and 10), and the chemical composition of the monimolimnia of meromictic lakes (Armstrong and Schindler unpublished data) indicated that Ca was equal to and sometimes greater than Na in solution. This impasse may be partially resolved by considering atmospheric dust to be an important source of Ca in the form of Ca–montmorillonite, possibly from the western prairies (Table 6). Montmorillonite would not be stable in these waters and should decompose to kaolinite, Ca, some Na, and Si. Montmorillonite collected from snow of ELA was well crystallized and resembled that in suspended sediment of the Red River at Winnipeg, whereas montmorillonite in the lake sediments was poorly crystallized and was probably in stages of decomposition. This speculation is based on scanty data and requires verification. A more likely source of Ca is from preferential solution of Ca from plagioclase.

The rather constant Fe:P ratio shown in Table 5 and in Fig. 2 may be related to the presence of some Fe–P precipitate, but we failed to find any trace of iron phosphate or iron sulfide minerals by X-ray diffraction on various size fractions of soil or lake sediment. We were able to extract from 110 C dried sediments 85–95% of ΣFe (Table 4) with hot 1 N HCl in 5 hr, but obtained only 8–15% of ΣP by this and other extraction procedures. About 10–30% of ΣAl was extracted in acid at room temperature from these sediment samples. This experiment suggests that a major fraction of P may not be associated with Fe and Al as a discrete mineral in ELA sediments. Although P is inversely related to ash content of the lake sediments (Fig. 1), P does not appear to be clearly related to C or N. The state of P in these profundal sediment samples is not known and requires further study.

The relatively high percentage of organic carbon (10–30% dry weight) does not imply great biological production in ELA lakes or watersheds; it is more likely due to: (*a*) lack of dilution by clastic materials; and (*b*) the probable abundance of resistant terrestrial soil organic material in ELA sediments. Schindler (1971b) advanced a general hypothesis concerning relations between the size of the drainage area in proportion to lake volume, theoretical water renewal times (τ) for ELA drainage systems, and characteristics of lake waters. Lakes that have large drainage basins in relation to their volume and surface area should have low values of τ, should receive more dissolved matter, and should deliver more suspended matter to their sediments. Since much of the particulate allochthonous matter in surface runoff is organic material (forest litter and soil particles), more organic material should be stored in the sediments of lakes with low values of τ. Figure 3 indicates the relation between percentage sedimentary organic carbon (Table 7) in ELA lakes and computed τ (table 5 in Brunskill and Schindler 1970). Only headwater lakes were included, so that neither inflow nor τ was modified by other lake basins. The correlation coefficient was 0.52, significant at the 1% level. Total nitrogen in these sediments may also be related to τ. The two lakes (241, 120) with low τ values (due to a large drainage basin in relation

to lake volume) are meromictic. True values of τ for these meromictic lakes are lower than indicated in table 5 of Brunskill and Schindler (1971), as the mixing volume of these lakes is about three-quarters of their total volume.

Ash content of these lake sediments was less clearly related to τ and no relation could be discovered between τ or any combination of drainage area–lake area–lake volumes, and the concentrations of Ca, Mg, Na, K, Si, Al, Fe, Mn, and P, in the lake sediments. This may not be surprising, as it would be more pertinent to know the total mass or mean mass per unit area of each element in the sediments. Data reported in Tables 4 and 7 represent profundal sediments only: many physical, chemical, and mineralogical properties of sediments should be related to water depth (see Table 8; also Frink 1969, 1967; Delfino et al. 1969; Nriagu 1968). At the low concentrations of dissolved ions in ELA lake waters (Armstrong and Schindler 1971) some fraction of the above-mentioned elements may be affected by plant metabolism or reactions involving humic acids. Varying amounts of Si would be retained in frustules of diatoms and *Equisetum* remains; Al is concentrated by various species of *Lycopodium* (Hutchinson 1945; Hutchinson and Wollack 1943; Lewin 1961, 1962).

C:N ratios for ELA lake sediments ($\Sigma C:\Sigma N$ = 9–14, Table 7) were all less than the C:N ratio for the soil sample ($\Sigma C:\Sigma N$ = 28.5, Table 3), which is typical of podzol or brunisol LF horizon soils. This may indicate some enrichment of N in the sediments from the lake water column, but much more data on soil chemistry are required to compare watershed soils to lake sediments. C:N ratios of ELA lake seston during 1969 were within the range 6–25 (Armstrong and Schindler unpublished data) and on the average were rather similar to sediment C:N ratios. C:P ratios in lake seston varied greatly from 100–300 in autumn, winter, and spring, to 1000–6000 in summer (Armstrong and Schindler unpublished data). The lake sediment C:P ratios of 130–380 (Table 7) are similar to the autumn, winter, and spring seston C–P composition. N:P ratios for lake seston in 1969 varied from 10–40 in autumn, winter, and spring, to 100–800 in summer (Armstrong and Schindler unpublished data). Lake sediment N:P ratios were much more uniform, within the range 11–32. The lake seston C, N, P data probably refer to suspended terrestrial debris and pollen, with algal cell materials a relatively minor fraction of the seston.

Table 12 shows the relation of ELA sedimentary parameters to some better known lakes of the world. At least for percent H_2O, L.O.I., C, N, and P, these ELA profundal sediment samples are very similar to published data on the sediments of the Wisconsin lakes, Linsley Pond, and small lakes of eastern Ontario in Shield and sedimentary drainage basins.

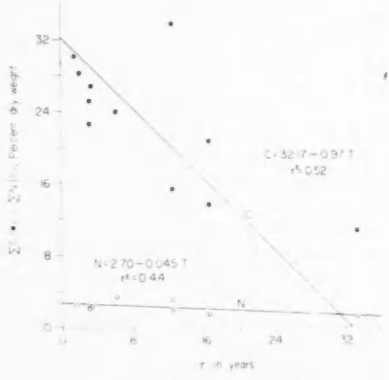

FIG. 3. Relation between sediment total carbon (ΣC, dots, % dry weight), total nitrogen (ΣN, circles, % dry weight) and theoretical water renewal time (τ, years), for selected ELA lakes.

Conclusions

1. The sediments of 16 small lakes in ELA are composed mostly of water, organic material, Si, and Al.

2. The primary (unweathered) minerals in the bedrock, soils of the drainage basin, and the lake sediments are (in rough order of abundance) quartz, plagioclase, K-feldspar, biotite or muscovite, or both.

3. Secondary (weathered) minerals in the soils of the drainage area and lake sediments are (in rough order of abundance) illite, chlorite, kaolinite, interstratified clay minerals of uncertain composition, and montmorillonite.

4. ELA drainage area soils and surficial deposits did not develop in situ: most of the sand and silt was brought into the area from the northeast, north, and northwest during periods of Pleistocene glaciation. Sediments suspended in the waters of glacial lakes were deposited in ELA.

5. Allochthonous clay minerals are concentrated by surface runoff in the lake sediments and are not in equilibrium with runoff water, lake water, or sediment interstitial water. These minerals should theoretically decompose to kaolinite, and should release cations (chiefly Ca, Na, K) and H_4SiO_4, and should remove H^+ from solution.

6. Based on preliminary estimates of annual runoff chemistry, precipitation, and evaporation, rates of weathering for Ca, Mg, Na, K, and Si were calculated as 44, 28, 46, 11, and 56 moles ha^{-1} $year^{-1}$ respectively, for the watersheds of lakes 239 and 240.

TABLE 12. Comparative surface sediment chemistry for ELA lakes and other well-known lakes. Samples are from near maximum depth. One standard deviation is given in parentheses for values from groups of lakes.

Lake		Water content (% *wet wt*)	Loss on ignition (% *dry wt*)	Organic carbon (% *dry wt*)	ΣN (% *dry wt*)	Kjeldahl N (% *dry wt*)	C:ΣN (*moles*)	ΣP (% *dry wt*)	Reference
ELA[a]	max	97	62	34	3.5	2.7	14	0.33	
	mean	94±2.7	44±14	20±0.7	2.1±0.8	1.8±0.6	12±2	0.22±0.05	c
	min	88	18	8	0.90	0.77	8	0.13	
Mendota, Wis.		~90	–	10	–	0.8–1.4	11.7[b]	0.1–0.2	d,e,f,g
23 Wis. lakes	max		64	40	–	2.52	18.6[b]	0.31	
	mean	~65–90	46	20±10	–	1.8±0.68	12.9[b]	0.12±0.09	d,e,f,g,h
	min		30	6.6	–	0.60	12.6[b]	0.011	
Linsley Pond, Conn.		–	30–40	–	–	~2.4	–	0.29	i,j,k,l
Bantam L., Conn.		90	28	–	–	1.4	–	0.27	x
L. Washington, Wash.		86	23	5	0.87	0.80	6.7	0.50	m,y
Fern L., Wash.		92	32	–	–	–	–	0.022	z
L. Erie		~70	35	3.0	0.3	–	11.7	0.08	n
L. Ontario		~70	–	4.0	0.4	–	11.7	0.19	n
4 E Ont. Shield lakes		93	–	29.4±5	–	2.3±0.25	14.9[b]	0.13±0.06	o
30 E Ont. sedimentary watershed lakes		76±16	–	20.6±13	–	1.8±1.0	13.4[b]	0.11±0.08	o
Windermere, S basin		–	20	8	–	–	–	–	p
Esthwaite		–	29	13	–	1.1	11.7[b]	0.20	p
Ennerdale		–	19	7	–	–	–	0.12	p
Buttermere		–	21	8	–	0.75	10.5[b]	–	p
Zürichsee, Switz.		78	–	10	–	0.35	33[b]	0.20	q
Biwa-ko, Jap.		–	8	1.1	–	0.22	5.8[b]	0.03	r
Yogo-ko, Jap.		–	18	4.5	–	0.68	7.7[b]	0.24	r
Haruna, Jap.		–	17	–	–	1.2	–	0.02	s
Suwa, Jap.		–	17	4.3	–	0.54	9.3[b]	–	s
Kizaki-ko, Jap.		72	20	4.4	–	0.50	10.3[b]	0.08	t,u
Kyrösjärvi, Finland		–	47	30	–	0.15	233?[b]	–	v
Sarkkilanjärvi	"	–	12	4	–	0.28	16.7[b]	–	v
Jalanti	"	–	13	3	–	0.25	14.0[b]	–	v
Mikolajki, Poland		95	11	6	–	0.70	10.0[b]	–	w

[a]Those ELA lakes discussed in this paper.
[b]C:Kjeldahl N.
[c]This report.
[d]Delfino et al. 1969, and Wentz and Lee 1969.
[e]Hasler 1963.
[f]Black 1929.
[g]Twenhofel 1933.
[h]Juday et al. 1941.
[i]Livingstone and Boykin 1962.
[j]Vallentyne and Swabey 1955.
[k]Deevey 1942.
[l]Hutchinson and Wollack 1940.
[m]Edmondson 1969, and personal communication.
[n]Kemp and Lewis 1968, and personal communication.
[o]Kleerekoper MS 1957.
[p]Mackereth 1965, 1966.
[q]Züllig 1955.
[r]Horie 1969.
[s]Saijo 1956.
[t]Koyama 1954.
[u]Sugawara 1957.
[v]Alhonen 1967.
[w]Wieckowski 1969
[x]Frink 1967.
[y]A. R. Abernathy, personal communication.
[z]Olsen et al. 1967

7. Concentrations of elements in sediment interstitial waters of holomictic lakes are greater than in overlying lake water; Fe, Si, and Ca are usually in highest concentrations. In meromictic lakes, there was little difference between monimolimnetic and interstitial water ion concentrations.

8. Phosphorus was inversely correlated with ash content in ELA profundal sediments, but was not clearly related to C or N.

9. Sediment carbon and nitrogen were directly related to theoretical renewal time in some headwater lakes.

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A Hypothesis to Explain Differences and Similarities Among Lakes in the Experimental Lakes Area, Northwestern Ontario[1]

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SCHINDLER, D. W. 1971. A hypothesis to explain differences and similarities among lakes in the Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Bd. Canada 28: 295–301.

A preliminary hypothesis is proposed to explain biological differences between Experimental Lakes Area (ELA) lakes in terms of simple morphometric and meteorological parameters, via their effect on nutrient supplies to the lakes.

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"Where the pieces have different and bizarre motions, with various and variable values, what is only complex is often mistaken (a not unusual error) for what is profound."

EDGAR ALLEN POE

MANY of the papers in this volume have included attempts to categorize or rank lakes, based upon one or a few components of the lake ecosystem (Schindler 1971; Schindler and Holmgren 1971; Patalas 1971; Hamilton 1971; Stockner 1971). Others provide data that are suitable for this purpose. A detailed examination of the above efforts reveals that although different components of the lake ecosystem are treated in each work, there is considerable agreement among the ranks or groups that were constructed by different authors. Since many of the proposed schemes are based upon morphometric parameters, I shall attempt to outline a simple hypothesis to explain the similarities in grouping upon morphometry in the first instance. (Morphometry as used here refers to physical characteristics of the whole catchment area, that is, both of the lake and of the terrestrial drainage to the lake.)

The Hypothesis

In recent years the view that nutrient supply to lakes is primarily responsible for differences in degree of eutrophy has received widespread acceptance (for example, Vollenweider 1968, 1969; Thomas 1970; International Lake Erie and Lake Ontario–St. Lawrence River Water Pollution Boards 1969), particularly when a broad variety of lakes is considered, including those influenced by man.

Phosphorus and nitrogen are almost always the limiting nutrients in Experimental Lakes Area (ELA) lakes (Sakamoto 1971; Armstrong et al. unpublished data; Schindler et al. unpublished data). Since ELA receives minimal quantities of the above nutrients from weathering by solution or human influences (Brunskill and Schindler 1971; Brunskill et al. 1971), and ELA is small and homogenous enough for precipitation to be similar over the area, one must conclude that the only important source of the above-mentioned elements is atmospheric precipitation (Armstrong and Schindler 1971; see also Bormann et al. 1968, and Schindler and Nighswander 1970, for data on other basins underlain by igneous or metamorphic rock). One must therefore assume that the relative quantity of nutrient supplied to a lake basin in ELA is directly proportional to its catchment area ($A_d + A_o$) (where A_d is the terrestrial portion of the drainage and A_o is the surface area of the lake) when the lake does not receive drainage from any other lake, i.e., is a headwater lake (as almost all of the small lakes studied in ELA are).

The nutrient in precipitation falling upon the terrestrial portion of the drainage basin is largely, though not entirely, assimilated by vegetation and soils (Armstrong and Schindler 1971; Schindler and Nighswander 1970). If one assumes, however, that the vegetation and soils are in some sort of equilibrium with the nutrient supplied by precipitation, the long-term average amount of nutrient entering a lake from a square meter of terrestrial drainage should be nearly equal to that falling

[1]The final paper in a series of 14 papers on the work of the Fisheries Research Board of Canada, describing background environmental data on the Experimental Lakes Area, northwestern Ontario. For location of numbered lakes see insert map at the back of this issue of the Journal of the Fisheries Research Board of Canada. A key to locations is given by Cleugh and Hauser (1971).

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upon the square meter, i.e., nutrient released to the lake waters as dissolved and suspended organic matter should equal that in precipitation. Transport of nutrients by wind and animals in such an extensive and homogenous forested area is likely to be negligible, or with imports to any basin equaling exports from it. The extent to which denitrification in Canadian Shield soils might affect nutrient retention in drainage basins is unknown. The fraction of nutrient released by decomposition in the terrestrial portion of the drainage that becomes available to aquatic organisms is also unknown. One must assume that a significant proportion of nutrients, particularly in particulate allochthonous matter, falls to the sediments without entering biotic cycles in the lake at all. Nevertheless, for elements with no gaseous phase, such as phosphorus, that have a high rate of turnover in biotic communities (Rigler 1964; Phillips 1963), the assumption that the average yearly rate of supply to an ELA lake is directly proportional to the catchment area ($A_d + A_o$) of the lake is probably not far from correct.

Catchment area is not the only parameter that must be considered. The volume of a lake should also be of primary importance, since for a catchment area of given size, any nutrient entering from precipitation or runoff will be diluted in proportion to the volume of the lake.

To summarize, one would expect the quantity of nutrient entering a lake per unit time to be directly proportional to the catchment area ($A_d + A_o$) and inversely proportional to the volume (V). If this is so, the level of biological productivity in the lake should be proportional to $\frac{A_d + A_o}{V}$.

Some crude tests of the above hypothesis are possible in ELA. The parameters A_d, A_o, and V for several ELA lakes are given by Brunskill and Schindler (1971). If the hypothesis is true, a significant, positive correlation should be detectable between $\frac{A_d + A_o}{V}$ and nutrient levels in ELA lakes, or between $\frac{A_d + A_o}{V}$ and any parameter that is dependent upon nutrient conditions (phytoplankton biomass, chlorophyll, production, etc.).

I shall begin by comparing the total mass of nutrient present in the water masses of several ELA lakes, including both suspended and dissolved fractions. This was obtained from the following calculation:

$$C_{\bar{x}} = \frac{1}{V} \int_{z=0}^{z=z_m} A_z \, C_z \, dz \qquad (1)$$

where $C_{\bar{x}}$ is the average quantity of nutrient (dissolved + suspended) per unit volume of lake, and C_z is the concentration at depth z. Although such a calculation would be most appropriate at

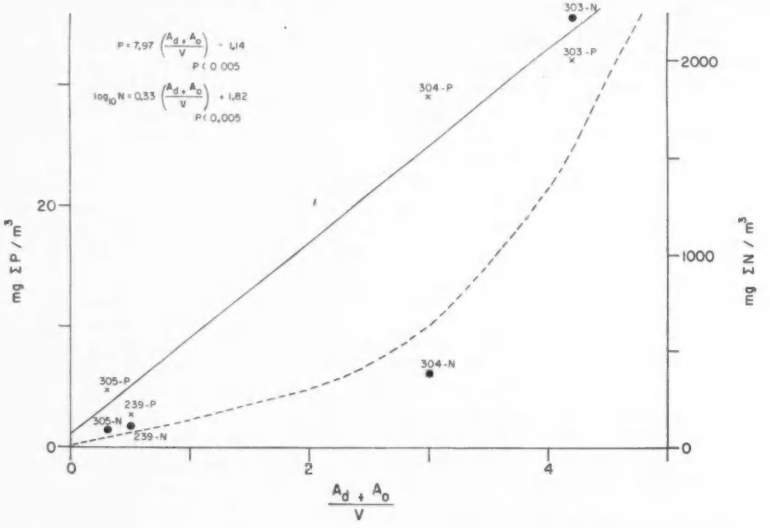

FIG. 1. Relation between the mass of total (dissolved + suspended) nitrogen and phosphorus in the water column and $\frac{(A_d + A_o)}{V}$.

spring overturn, when the runoff from A_d is maximal and there is little possibility of short-term sedimentation, the only data available for all nitrogen and phosphorus fractions are, unfortunately, from the height of summer stagnation. Results are shown in Fig. 1, along with the results of a test for the significance of b, the regression coefficient.[2]

Figures 2, 3, and 4 show several indices of phytoplankton biomass and production in relation to $\frac{A_d + A_o}{V}$. Data are taken from Schindler and Holmgren (1971). All of the relations fit well.[3]

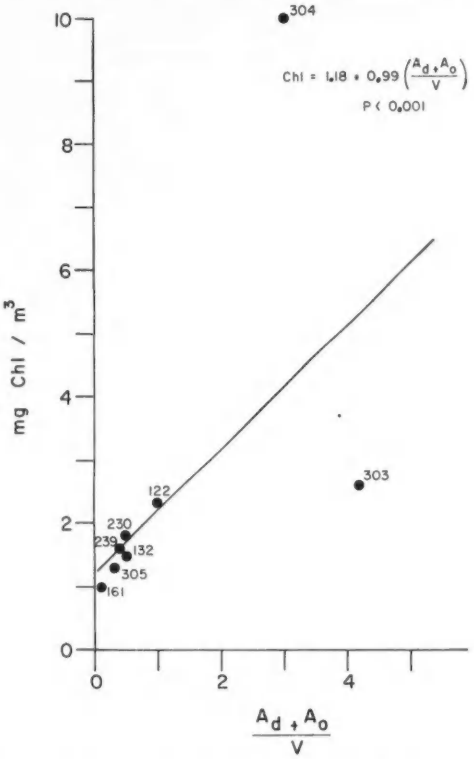

FIG. 2. Relation between average chlorophyll/m³ in the euphotic zone and $\frac{(A_d + A_o)}{V}$.

[2]The same test is performed on each figure that follows.

[3]Although no data are currently available, I suspect that phytoplankton standing crop and production would not show the relation predicted above if lakes were strongly colored enough to limit light penetration to the upper few centimeters of the water column (>70 Pt. units).

Stockner (1971) showed that the ratio of the diatom tribe Araphidineae to the order Centrales may be a sensitive indicator of stage of eutrophication. If the reasons for this are assumed to be

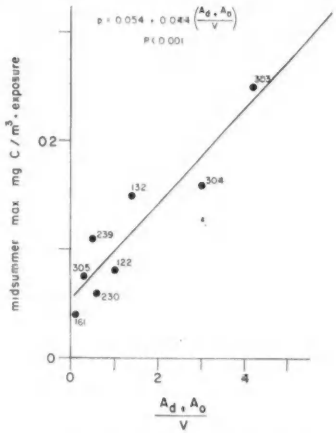

FIG. 3. Relation between midsummer phytoplankton production (euphotic zone average) and $\frac{A_d + A_o}{V}$ phytoplankton biomass.

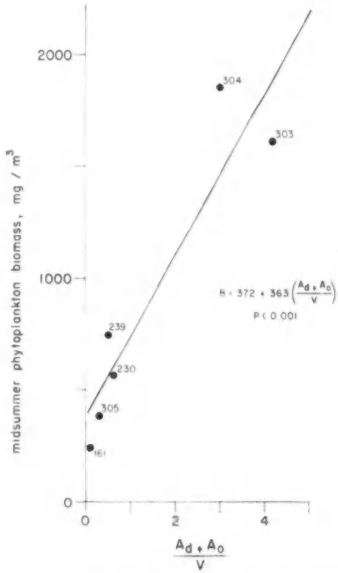

FIG. 4. Relation between phytoplankton biomass (euphotic zone) and $\frac{(A_d + A_o)}{V}$.

related to nutrient conditions, a significant relation with $\frac{A_d + A_o}{V}$ would again be expected. The regression coefficient is significant (Fig. 5).

Several other measurements that have been traditionally done in limnological survey work, including that in ELA, are affected both by lake metabolism and by allochthonous material entering from the terrestrial drainage of the lakes. These include oxygen deficits (Schindler 1971), sedimentary carbon, and sedimentary nitrogen (Brunskill et al. 1971). One would expect such measurements to be closely correlated with $\frac{A_d + A_o}{V}$, since total organic production in the terrestrial drainage and nutrients in runoff as well as in the lake contribute to them. The relation between $\frac{A_d + A_o}{V}$ and the three above-mentioned measurements in several ELA lakes is shown in Fig. 6–8. Once again, the relation would be expected to apply only for an area such as ELA, where the "yield" of organic material or nutrient per unit area of terrestrial drainage is likely to be similar for all basins, since terrestrial communities and soils in most basins are quite similar, at least superficially.

If the soils and vegetation of terrestrial drainages are relatively homogenous, one other relation would be expected. All small streams in ELA, which drain areas that do not include lakes, appear to be relatively high in humic color. This colored water would be diluted by rainwater that falls directly on the lake surface, but otherwise the color is quite stable. Color measurements done in fall 1968, and winter 1970, in ELA lakes demonstrated that in the absence of inflow the humic color of lake water changes very little (Fig. 9). The color of lakes, again assuming for simplicity that rainfall and terrestrial vegetation and soils are uniform, should be proportional to the area of terrestrial drainage per unit lake surface (A_d/A_o)[4] (see Fig. 10). The color and hence the transparency of lakes appears to be largely a function

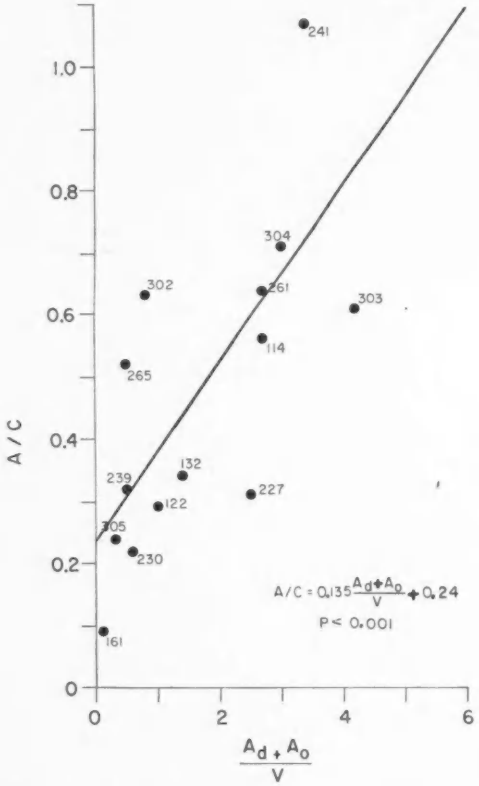

FIG. 5. Relation between the Araphidinae–Centrales ratio in sediments and $\frac{A_d + A_o}{V}$.

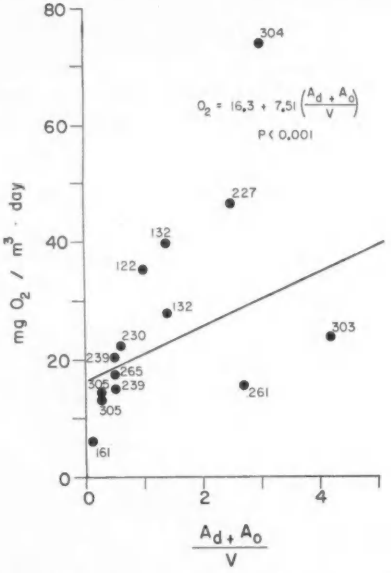

FIG. 6. Relation between rate of winter oxygen depletion and $\frac{(A_d + A_o)}{V}$.

[4]Assuming that lake evaporation and terrestrial evapotranspiration, which would tend to intensify the color, are equal.

of the proportion of water input received from terrestrial drainage.

Unfortunately, it is impossible to evaluate the above hypothesis in terms of animal populations. The number of lakes treated by Schindler and Novén (1971) is insufficient, and the works of Hamilton (1971) and Patalas (1971) are based upon relative species abundance rather than quantities of animals per unit volume. A simple comparison of even these relative quantities is, however, revealing. The species composition categories of both latter authors are set out in relation to $\frac{A_d + A_o}{V}$ in Fig. 11. The classes A and C–F of Hamilton separate nicely with respect to $\frac{A_d + A_o}{V}$. If one considers the area of overlap between classes II, III, and IV on Patalas's fig. 5 as a separate category, the same may be said of his classification scheme. The exception in both instances is the category that includes lakes 230 and 241 (category B of Hamilton, and IV of Patalas). This category overlaps

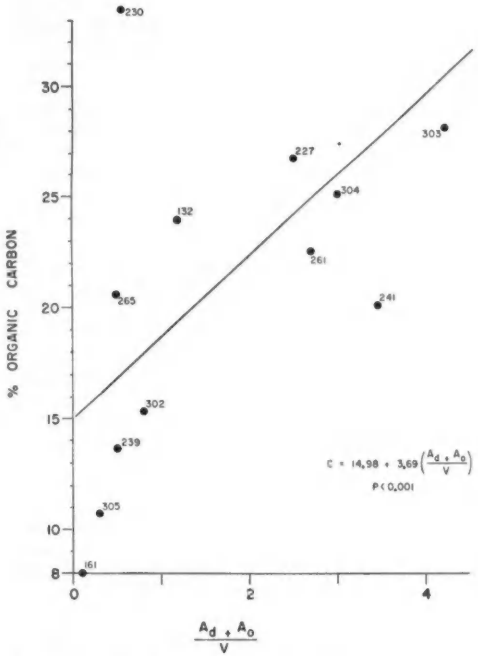

FIG. 7. Relation between organic carbon in sediments and $\frac{(A_d + A_o)}{V}$.

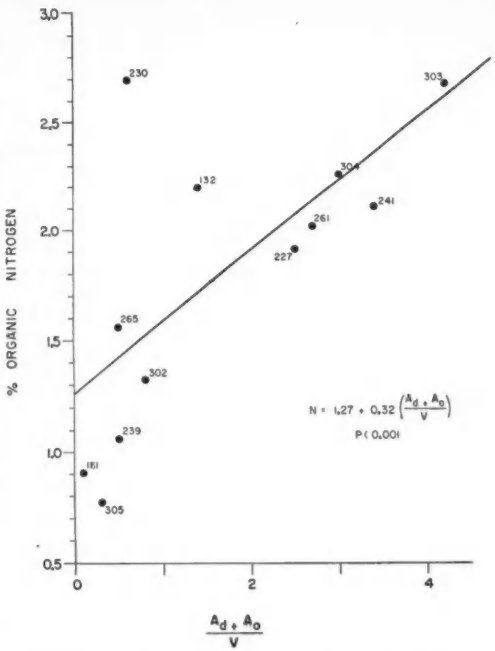

FIG. 8. Relation between organic (Kjeldahl) nitrogen in sediments and $\frac{A_d + A_o}{V}$.

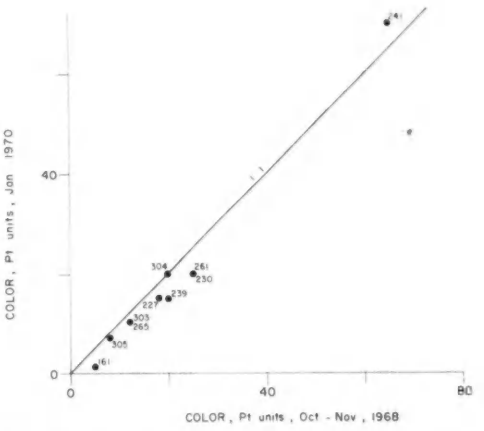

FIG. 9. A comparison of water color measurements (filtered samples) done in October 1968 and January 1970. The diagonal line represents perfect agreement between the two sets of measurements.

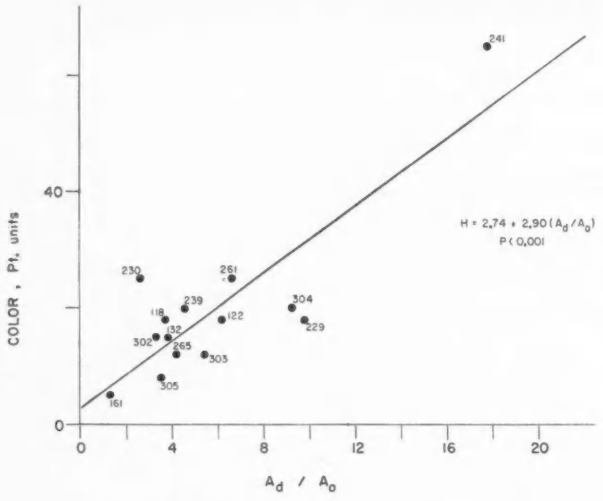

FIG. 10. Relation of water color to the ratio of A_d/A_o.

a broad range of $\frac{A_d + A_o}{V}$ and seems unlikely to be related to the hypothesis. The small size and relatively great depth (average slope = 0.187 and 0.168 for lakes 230 and 241, respectively) of these two lakes may be more important influences than nutrient supply, since they are by far the smallest, most protected, and most steeply sloping basins in ELA (range of A_o for other lakes treated in this paper = 4–1007 ha, with average slopes of 0.014–0.110).[5]

If the above simple hypothesis is generally true, changes in lake morphometry should cause changes in the nutrient regime of a lake. The most common change to be expected is the filling of the lake basin with sediment as a lake ages. By reducing the lake volume, the ratio $\frac{A_d + A_o}{V}$ and hence the nutrient per unit volume, should be increased. During a period of years when precipitation and other meteorological conditions are relatively uniform, one should be able to assume that lakes with different ratios $\frac{A_d + A_o}{V}$ represent different successional stages. If correct, this prediction should provide a powerful tool for evaluating the effect of artificial enrichment upon lakes.[6]

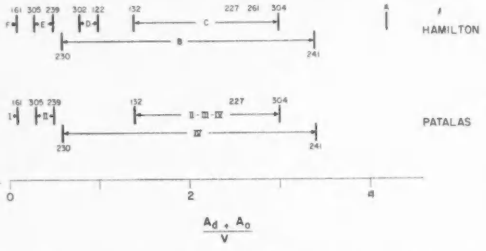

FIG. 11. A comparison of the categories of Patalas (1971) and Hamilton (1971) with $\frac{A_d + A_o}{V}$.

[5]Average slope is defined as $\frac{z_m}{\sqrt{A_o/\pi}}$.

Acknowledgments

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[6]One must consider the above to be an "open" hypothesis in the sense of Schlesinger (1963), i.e., one that will not be proven or disproven in one test, but that must be subjected to continuous revision and restatement as better information becomes available.

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